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Published at the Museum of Zoology, The University of Michigan, Ann Arbor, and the University of Colorado Museum, Boulder, by the Society for Experimental and Descriptive Malacology.

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ON THE COVER – Land snails of upper Michigan. Illustrations by John L. Tottenham.

1986

M70A-13

MALACOLOGICAL REVIEW

19 (1-2)

1986

MALACOLOGICAL REVIEW

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MALACOLOGICAL REVIEW

VOLUME 19, Number 1-2 1986

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Malacological Review, 1986, 19: 1-43

POLYMORPHISM IN *CORBICULA FLUMINEA* (BIVALVIA: CORBICULOIDEA) FROM NORTH AMERICA

Joseph C. Britton and Brian Morton

ABSTRACT

Evidence recently has appeared suggesting that more than one species of *Corbicula* occurs in North America. In addition to the typical *C. fluminea*, characterized herein (Form A), there is a second *Corbicula* morphotype (Form B) characterized by dark periostracum and a darkly pigmented shell interior, more closely spaced concentric sulcations in young specimens, and a slightly narrower body. We found Form B in North America usually restricted to permanently flowing, oligotrophic, calcium and carbonate-rich, often spring-fed and travertine depositing streams in arid, warm temperate environments. A similar morphology also is known to occur in *C. fluminea* from flooded furrows of Hong Kong vegetable gardens.

Comparative population, morphometric and reproductive studies of Forms A and B were conducted. Sulcation spacing on the shell exterior serves to differentiate Form A and B morphotypes less than 15 mm in length, but becomes unreliable for morphotype discrimination on larger specimens. Arcsin transformed shell dimension ratios (calculated from length, height and width measurements) demonstrate low intrapopulation variability, but moderate to considerable difference between populations separated by space or time. Differences are most apparent between Form A and B morphotypes, but also are commonly significant ($p < .05$) among Form A or B comparisons. Large samples of sympatrically distributed Form A and B morphotypes displaying significantly different mean dimension ratios also display considerable overlap with respect to these ratios. These data support the concept of self-fertilization as an important reproductive mechanism (producing low variability within populations). Because of some outbreeding, however, differences between populations with low internal variability are more apparent than would be if each population displayed somewhat greater variability. We conclude that shell dimension comparisons are unreliable for taxonomic discrimination in *Corbicula*.

The restricted, habitat-correlated distributions of Form B *Corbicula*, the presence of intermediate morphologies when some but not all environmental conditions normally associated with Form B are present, and the virtual absence of Form B in localities where conditions normally associated with this morphotype are absent are strong indications that the Form B morphology is a habitat-specific response derived from the predominant (Form A) North American phenotype. In addition to differences in shell morphology, Forms A and B also display differences in sexual expression which may be an effect of habitat. The tendency for *C. fluminea* to develop different reproductive strategies in different environments may reinforce phenotypic differences between morphotypes.

We conclude that there is still insufficient evidence to justify a two-species model for North American *Corbicula*. The preponderance of evidence supports the view that a single highly variable species, *C. fluminea*, is the only introduced corbiculid in North America.

INTRODUCTION

Corbicula is conservative, possessing relatively few morphological characters useful for species discrimination and displaying a broad range of subtle variability, especially with respect to shell form and color. Early conchologists (including Heude, Prashad, Prime, and others) considered slight differences in shell morphology between native Asian, Australian, eastern European and African populations sufficient to justify a plethora of species names. Most of the Asian names, and possibly many from other parts of the natural range, can, however, be synonymized into two groups (Morton, 1979; 1986): the freshwater *C. fluminea* Müller 1774 and the estuarine *C. fluminalis* Müller 1774. Only the former species has been introduced into North America (Britton & Morton, 1979; Morton, 1979), where it is a pest of potable and industrial water supply systems (Sinclair & Isom, 1963; Eng, 1979).

Recently, Fontanier (1982), working on the distribution of *Corbicula* in the Brazos River system, Texas, discovered what he described as a dark phase morphotype coexisting with the typical *C. fluminea* in southern portions of the drainage. These specimens are very similar to other dark specimens collected at several localities throughout the southwestern United States and figured by Sinclair & Isom (1963: pls. 2, 7). Similar morphotypes occur in lotic environments in Hong Kong.

Hillis & Patton (1982) investigated the two Brazos drainage "forms" and showed that they had fixed homozygous allelic differences at six of 26 genetic loci. In view of these data and certain morphological

differences observed between the two forms, Hillis and Patton concluded that the single species concept for North American *Corbicula* populations proposed by Britton & Morton (1979) could no longer be justified. They refrained, however, from assigning the dark morph to an existing nominal species or proposing a new name for it.

In 1979, one of us (JCB) independently discovered a population of *Corbicula* containing two color morphs (i.e., the light and dark forms of Fontanier, 1982) in Pinto Creek, Kinney County, Texas. In September 1981, we were able to begin a study of the Pinto Creek population with additional material for comparative purposes collected from several other localities. The purpose of this research is to resolve the issue of whether there is one or more species of *Corbicula* in the southwestern United States.

TAXONOMY

Most "species" of *Corbicula* exist only as museum types. The most recent conchological revision of *Corbicula* was by Prashad (1924; 1928a,b; 1929; 1930), although Morton (1979), using Prashad's own analyses, demonstrated that the genus was overburdened with nominal species. Populations have rarely been studied within the natural range of the genus. Where they have, however, two species are clearly separable. Accordingly, Morton (1986), after consideration of ecological, physiological, population and reproductive data from China and Japan, reaffirmed **on the evidence available** that but two species of *Corbicula* occur throughout Asia, namely *C. fluminea* and *C. fluminalis*. These species are separable over a wide range of characters. Although difficult to distinguish by shell morphology when young, adult *C. fluminalis* (> 1 yr) bear deeply impressed growth lines in addition to widely spaced sulcations on the shell exterior, whereas more closely spaced sulcations and indistinct growth marks appear on shells of *C. fluminea*. *C. fluminalis* also tends to be taller (less elongate) than *C. fluminea*.

Several less obvious or non-morphological features better serve to distinguish these species (Morton, 1977; 1982; 1983). *Corbicula fluminalis* lives up to 10 years, usually is found in the brackish lower reaches of river mouths, is a winter breeder with one generation per year, and is non-incubatory and dioecious with a trend towards protogyny. It possibly can tolerate salinities up to 24 ppt (Kado & Murata, 1974). In contrast, *C. fluminea* is a freshwater species rarely found naturally in salinities over 1-2 ppt. It cannot tolerate prolonged exposure to salinities in excess of 13-15 ppt (Gainey & Greenberg, 1977; Evans et al., 1979; Morton & Tong, 1985). Its lifespan rarely exceeds three years, it breeds in spring and fall, and it broods eggs in the inner demibranchs to a 200 μm pediveliger stage. *C. fluminea* also is characterized by an extremely variable shell morphology and a capacity to occupy a wide variety of freshwater microhabitats, occurring with equal facility in both lentic and lotic waters. As will be seen, the shell plasticity of *C. fluminea* may be directly or indirectly correlated to this species' eurytopicity.

Scanty evidence from other parts of Asia suggest that everywhere *Corbicula fluminea* possesses the same array of characters. Two other nominal species, *C. japonica* Prime 1864 and *C. leana* Prime 1864 of Japan, despite different names, display essentially the same range of characters as *C. fluminalis* and *C. fluminea* respectively (Morton, 1986), as do many of the numerous other nominal species of mainland Asia and insular southeastern Asia (Morton, 1979).

Despite this apparent clarification of the *Corbicula* species group in Asia, the picture is confused by the fact that both species attain different maximal sizes over their wide ranges. Whereas in southern China, *C. fluminalis* is much larger than *C. fluminea* (maximum lengths of 54 mm and 35 mm respectively) (Morton, 1986), the opposite **seems to be** the case in northern Asia (maximum lengths of 21 mm and 37 mm respectively) (Zhadin, 1965). Maximum shell size is probably species variable (as Morton, 1969, showed for *Dreissena polymorpha*) and may be different in different populations over its range. This is probably a temperature-related effect (Alimov, 1974).

Throughout its range, *Corbicula fluminea* is biologically variable. If this is also true of *C. fluminalis* (yet to be investigated in the same detail), then, bearing in mind the intrinsic shell conservatism of the genus as a whole, interpopulation variability is likely to be high. Such variability is compounded by the fact that within a single river system the range of the two species may overlap (facilitated by salinity tolerances of both species). When sympatrically distributed, juveniles of *C. fluminalis* are difficult to distinguish from *C. fluminea*.

Corbicula was introduced into North America during the first half of this century (Burch, 1944; Counts, 1981). In light of the confusion surrounding the taxonomy of Asian populations, it is not surprising that several names initially were applied to North American *Corbicula* during the subsequent spread across the continent (Britton & Morton, 1979). In a review of the characteristics and literature pertaining to introduced North American *Corbicula*, Britton & Morton (1979) concluded that but one

species had been introduced, the freshwater *C. fluminea*. As with Asian populations, North American *C. fluminea* displays considerable variability in shell morphology, as well as in size, growth rate, reproduction and some aspects of physiology (Mattice & Dye, 1975; Aldridge & McMahon, 1978; Gainey, 1978a,b; Britton & Morton, 1979; Britton et al., 1979; Eng, 1979; Sickel, 1979).

The maximum size attained by *Corbicula* in North America varies greatly, often according to habitat. As in southern China (Morton, 1977), most American *Corbicula* have a length less than 35 mm and live less than three years. Larger, longer-living specimens usually are found in relatively protected waters not subjected to intermittent flow, catastrophic flooding or reservoir drawdown (Bickel, 1966; O'Kane, 1976; White, 1979). Under these conditions, length may exceed 50 mm (Eng, 1979). Shell shape also may be modified according to habitat. For example, shells tend to be more elongate and slightly narrower in fast flowing water, more rounded and globose in still or sluggish flows (Britton & Morton, 1979, figs. 7, 10, pp. 265, 271). Environment also may influence the number or degree of elevation of concentric shell sulcations (Britton & Morton, 1979, fig. 5, p. 262), or the degree of pigmentation of the shell interior, exterior, or both (see below).

Asian and North American *Corbicula fluminea* breed twice a year (spring and fall), with eggs retained in the inner demibranchs until release as pediveligers. The literature has recorded a discrepancy, however, as to the sexuality of Asian and American *C. fluminea*. Morton (1977), using gonad smears for analysis, found *C. fluminea* from Plover Cove Reservoir, Hong Kong, to be a protandric consecutive hermaphrodite. North American populations have been reported by most workers to be simultaneous hermaphrodites with seasonal production of sperm (Heinsohn, 1958; Kraemer & Lott, 1977; Eng, 1979; Kraemer, 1979). Japanese workers also consider *C. fluminea* (= *C. leana*) to be a simultaneous hermaphrodite (Ikematsu & Yamane, 1977; Fuziwara, 1979). Morton (1983) examined stained sections of lotic and lentic populations of Hong Kong *Corbicula* and discovered a partial explanation for this discrepancy. The sexuality of Hong Kong *Corbicula* is influenced by the environment in which the animal lives. In lentic waters, such as Plover Cove Reservoir, the population consists of approximately equal proportions of males, females and hermaphrodites. By contrast, no males exist in populations of *C. fluminea* from lotic flooded furrows, the population comprising approximately equal numbers of females and hermaphrodites. Maleness and free-shedding of sperm are presumably less efficient for propagation of the species in flowing water than is self-fertilization, the latter method producing a large number of offspring without the risk of gamete loss. We will show in this paper that, as in Hong Kong, the sexuality of North American populations also may vary according to habitat, and we will discuss the possible genetic consequences of a variable sexuality.

The genetics of Asian *Corbicula* are poorly known. Smith et al. (1979) examined material from Japan, Hong Kong and the Philippines, as well as several North American localities, and concluded that the absence of genetic variability among North American *Corbicula* was likely the consequence of a small founding invasive population. Subsequent work, although finding greater genotypic variation still supports the small founding population model for the *Corbicula* colonization of this continent (McLeod & Sailstad, 1981; Hillis & Patton, 1982; McLeod, 1986).

METHODS AND MATERIALS

Corbicula fluminea were collected for population and reproductive studies at two Texas localities. For 20 months, from September 1981 to April 1983, samples were collected at approximately monthly intervals from Pinto Creek, Kinney County, Texas, at the U.S. Highway 277 bridge (Fig. 5). From September 1981 to May 1982, similar samples were taken from the Brazos River, Sommerville County, Texas, at approximately 30 river km downstream from DeCordova Bend Dam. (The Brazos River collections were terminated when late spring flooding made the study area inaccessible for almost three months and destroyed most of the *Corbicula* population.) At both localities, specimens were collected by screening large quantities of sediment through a series of sieves, terminating with a 1 mm mesh. All specimens retained by the screens were collected until the sample size exceeded 500 individuals. Pinto Creek samples were designated as either dark or light morph, according to criteria discussed below. Intermediates were always assigned to one or the other category; no questionable phenotypes were discarded. Shell lengths were determined to the nearest 1 mm for each subpopulation, and size-frequency histograms were plotted, the number of specimens in each 1 mm size class being expressed as a percentage of the total number in each subsample. Similar procedures were followed for Brazos specimens, except that no light or dark subpopulations were differentiated.

Five specimens at each mode of the frequency distribution of each subpopulation from each sampling period at Pinto Creek, and each sampling period from the Brazos, were preserved in Bouin's fixative for histological examination. These were sectioned at 6 μm through the center of the body, stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome, and the gonads were closely examined to determine sexuality.

Several additional collections of *Corbicula* were made at various localities for comparative purposes as follows. (1) From December 1982 to March 1983, an intensive survey of the distribution of *Corbicula* in Pinto Creek was conducted and hydrological data collected. Sample localities are shown in Fig. 5. Additional material also was collected from (2) an irrigation canal near Montezuma Well, Montezuma Castle National Monument, Arizona, in October 1982

(Fig. 6); (3) from several localities in the vicinity of the Phoenix, Arizona, County Club golf course (Fig. 7); and from (4) flooded irrigation furrows at several localities in the New Territories, Hong Kong, during 1982 and 1983. The Montezuma Well *Corbicula* consisted exclusively of specimens corresponding to the dark morph seen in Pinto Creek, whereas Phoenix *Corbicula* included both color morphs. Specimens from Hong Kong display variability of external shell morphology, and can be separated into light or dark morphotypes similar to those seen in Pinto Creek. Hydrologic data for the Brazos River were taken from literature reports (U.S. Geological Survey, 1981; 1982; 1983).

Samples from each of the above populations were utilized for several kinds of morphometric analysis. Length, height and width of specimens were determined to the nearest 0.1 mm. Height/length, width/length and width/height ratios were calculated and arcsin transformed for additional analysis. Analyses of variance were performed for all populations and for light and dark subpopulations. In all cases, variances were shown by Bartlett's test to be heteroscedastic. Thus, the approximate test of equality of means (Sokal & Rohlf, 1981) was performed on pairs of means.

The number of sulcations per millimeter of shell surface were determined for specimens from Pinto Creek and Montezuma Well irrigation canal. The number of sulcations per 5 mm were determined along a vertical distance extending 15 mm from the ventral margin toward the umbo. The ventral-most 5 mm segment was discarded as its variance suggested that this measurement was unreliable. The number of sulcations per mm were calculated for each of the subsequent 5 mm segments. In this manner, variation in the number of sulcations per mm could be assessed in relation to variation in total shell size.

RESULTS AND IMMEDIATE CONSIDERATIONS

Shell morphology and morphotypes

Asia

Two color morphs of *Corbicula fluminea* occur in the flooded furrows of Hong Kong vegetable gardens. The majority of individuals in these populations have straw yellow or cream colored shells with typically widely spaced concentric ridges (Pl. 1, Fig. A). Juveniles have tiny flashes of purple located to either side of the umbones. The shell interior usually is uniformly cream or white, although some specimens may display light purple streaking. These features also characterize many North American *Corbicula*. Some Hong Kong specimens also display radiating streaks of orange-brown on various parts of the shell exterior (Pl. 1, Fig. A, arrows).

A dark morph (Pl. 1, Fig. A) coexists with the typical *Corbicula fluminea* in some Hong Kong furrows (e.g., in the Lam Tsuen Valley). The flashes of color present on juvenile shells progressively enlarge as these specimens age. By the time the shell attains a length of 5-7 mm, the shell becomes uniformly darkened. The shell interior also is colored uniformly moderate to light purple. As will be demonstrated for the American dark Form B, these dark morphs from Hong Kong have a subtly different shell form and are predominately hermaphrodite in contrast to the mainly female light morphs (Morton, unpubl. data).

Thus, in the natural Asian range and within the same environment, *Corbicula fluminea* has a capacity for shell variation, particularly with regard to color. When specimens from different habitats (Morton, 1983) or different geographic localities within the natural range (Morton, 1979; 1986) are considered, the degree of variability in shell morphology becomes even greater.

North America

The majority of the North American *Corbicula* (hereafter designated Form A) correspond to the light form described above from Hong Kong, except that North American specimens normally lack the orange-brown radiating lines and tend to have uniformly elevated concentric sulcations (Pl. 1, Fig. B). In a few localities (e.g., see Fig. 1), however, a distinctly different *Corbicula* morphotype occurs (Pl. 1, Fig. B). Like the dark Hong Kong morph, the North American variant is darkly pigmented, but the latter has several additional features which are not seen in the former. (To differentiate the Hong Kong dark form from that in North America, the former hereafter will be described as the "dark form", whereas the latter will be described as "Form B".) The shell of Form B tends to be narrower (less globose) and slightly more elongate than most typical *C. fluminea*. Form B also has more closely spaced concentric sulcations on the dorsal third to half of the shell, although, as the animal ages, sulcations become more widely spaced and the distance between sulcations becomes indistinguishable from that of "typical" *C. fluminea* (Fig. 2). Finally, as we will show, Form B seems to have a specific microhabitat **preference**, although as with most *Corbicula* populations it has **tolerance** for other microhabitats. In some localities, Form B is the only *Corbicula* present (e.g., in the Montezuma Well irrigation canal, see below), whereas in other localities it appears to be sympatric with the typical Form A (e.g., in the San Gabriel River as indicated by Hillis & Patton, 1982). As will be seen, however, the "sympatry" seems to be the result of varying conditions along a drainage which, in turn, influence the expression of different *Corbicula* morphotypes.

PLATE 1. FIG. A. *Corbicula fluminea* from irrigation furrows in the Lam Tsuen Valley, New Territories, Hong Kong. Left series, light morphotypes; right series, dark morphotypes. Note streaks of orange-brown color on both color forms (arrows). FIG. B. *C. fluminea* from locality N (see Fig. 5), Pinto Creek, Kinney Co., Texas. Left series, Form A; right series, Form B.

FIG. 1. Distribution of *Corbicula fluminea* in the United States. The shaded area represents the geographic distribution of the Form A morphotype. Letters indicate the known or reported occurrences of the Form B morphotype. **A,** Several localities in the lower Colorado River and Imperial valleys of southwestern Arizona and southeastern California, e.g., the Colorado River and Main Canal at Parker, La Paz Co., Arizona. **B,** Verde Valley, north-central Arizona. Specific localities include the Montezuma Well irrigation canal, Montezuma Well National Monument (see Fig. 6) and an irrigation canal traversing Clear Creek Campground southeast of Camp Verde, both in Coconino Co., Arizona. **C,** Phoenix, Maricopa Co., Arizona, and vicinity, including the following specific localities: Grand Canal of the Salt River Project at Osborne and 18th streets; supply canal from the Grand Canal to the Phoenix Country Club grounds along Osborne Street; ponds on the Phoenix Country Club (see Fig. 7); Eastern Canal at Gilbert Road; Southern Canal 0.2 km downstream from Roosevelt Canal pump station; and the Arizona Canal at the intersection with Arizona Highway 87, northeast of Mesa, Arizona. **D,** Pinto Creek, Kinney Co., Texas (see Fig. 5). **E,** East San Gabriel River, Williamson Co., Texas (Hillis & Patton, 1982). **F,** Little Brazos River, Robertson Co., Texas (Charles Golightly, pers. comm.).

Morphometric differentiation

Hillis & Patton (1982) employed an *a posteriori* morphometric analysis to distinguish between two apparently sympatric forms of *Corbicula* from the San Gabriel River, Texas. They showed that the two forms which they subjectively recognized to be different also could be shown to be distinct by morphometrics. In an attempt to confirm the Hillis and Patton observations by an analysis of specimens collected from the same locality from which they collected *Corbicula*, we searched the San Gabriel River, as well as several additional sites upstream and downstream, in September 1981. Unfortunately, San Gabriel River *Corbicula* had suffered a severe mortality during the preceding summer. We found no living specimens of either morph and very few shells. Thus, we can neither confirm nor deny Hillis and Patton's observations from this locality. The sparse shell material that was collected from the San Gabriel River, however, and abundant live material collected in October 1983 (after the termination of this study), permits us to confirm that the light and dark forms described by Hillis and Patton generally correspond to the Form A and B morphs described herein from Pinto Creek, Texas, and several Arizona localities.

To expand our understanding of the total variation in shell form of *Corbicula*, basic dimension ratios (height/length, width/length and width/height) were determined for samples of populations discussed herein, namely: (1) light and dark morphotypes from Hong Kong; (2) Forms A and B from Pinto Creek; (3) Form B from Montezuma Well irrigation canal; (4) Form A from the Brazos River; and (5) Forms A and B from the Phoenix Country Club site, Arizona. Mean values for these ratios are plotted in Fig. 3 in a manner similar to that undertaken by Hillis & Patton (1982). The dark *C. fluminea* from Hong Kong and Form B *Corbicula* from Pinto Creek, the Phoenix County Club and Montezuma Well irrigation canal tend to cluster together, distinct from a second cluster comprising

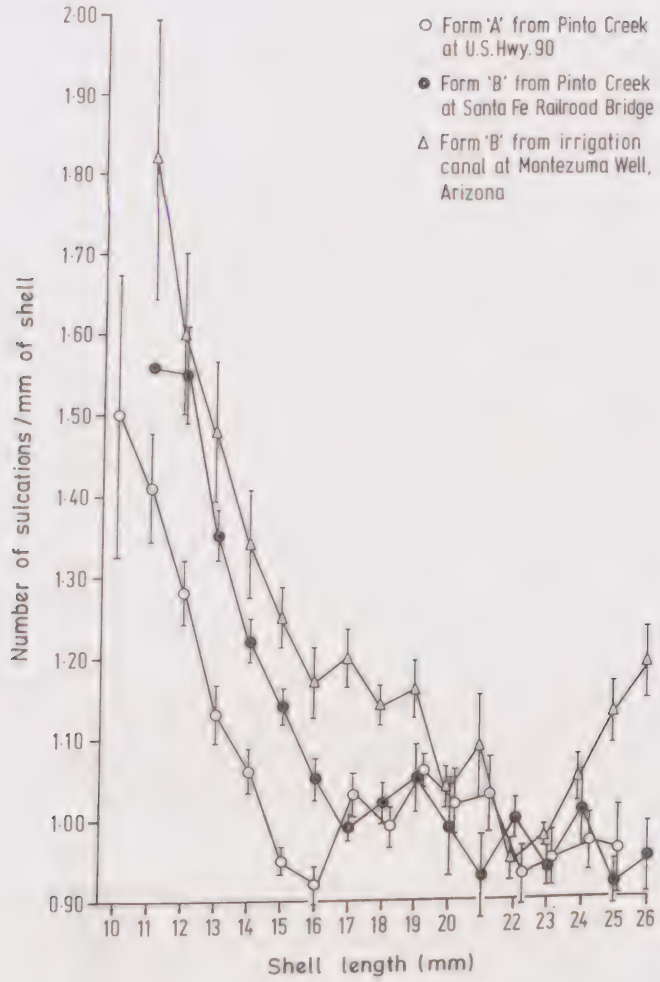

FIG. 2. The mean number of sulcations per mm of shell, measured perpendicular to length, on the shells of Form A and B morphotypes from Pinto Creek, Texas, and the Montezuma Well, Arizona, irrigation canal, and plotted in 1 mm length increments from 10 to 26 mm. Each point is the mean value for 10 specimens; bars indicate ± one standard error. The open circles represent Form A from Pinto Creek locality B (Fig. 5); the closed circles represent Form B collected from Pinto Creek locality I (Fig. 5); and the triangles represent Form B collected from locality H at Montezuma Well National Monument (Fig. 6).

the light form of *C. fluminea* from Hong Kong and Form A from the U.S. localities. By analysis of Fig. 3, we can characterize the former groups as thinner and more elongate than the latter.

Our data, therefore, seemingly support the morphometric analysis of Hillis & Patton (1982), suggesting two distinctive morphotypes among North American *Corbicula*. There is, however, a serious flaw in both analyses. Hillis and Patton's morphometrics and our Fig. 3 represent *a posteriori* analyses. Specimens were grouped according to preselected or preconceived criteria and then analyzed. Hillis and Patton state "twenty-five of each form were collected on 10 January, 1981, and another 25 of each were collected on 7 April, 1981." Clearly, they partitioned specimens into mutually exclusive groups **prior** to measurement. Whether or not possible intermediates were rejected to attain the test sample is not stated. We do not intend to imply that samples were selected deliberately to influence results. Indeed, from almost three years of experience in attempting to distinguish between Form A and B morphotypes, it is clear to us that intermediate forms not readily distinguishable as either morph are commonly encountered. When one attempts to separate a sympatric population into two mutually exclusive categories, there is a natural tendency to ignore or pass over intermediate forms for distinctly differentiated specimens.

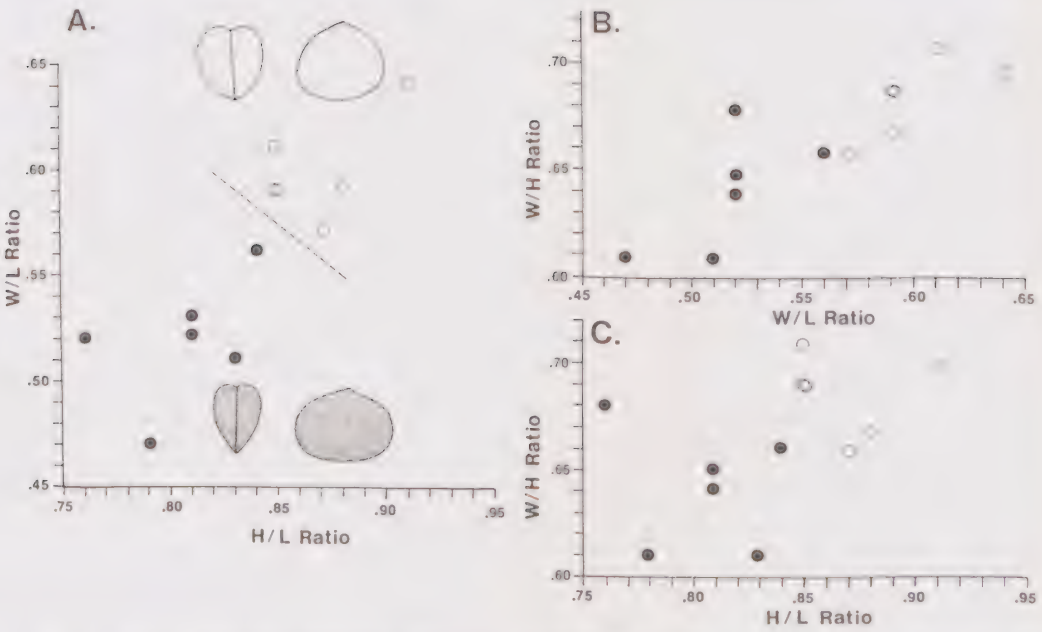

FIG. 3. Plots of mean shell dimension ratios for 12 populations of Form A (closed circles) or B (open circles) *Corbicula fluminea* listed in Table 1. **A**, Width/length ratio vs height/length ratio. The dotted line bisects the grand mean determined for all populations and serves to differentiate between the relatively globose and inflated Form A morphotype (illustrated above) from the more elongate and relatively thinner Form B morphotype (illustrated below). **B**, Width/height vs width/length ratio. **C**, Width/height vs height/length ratio. Note that all diagrams can be interpreted either as consisting of distinctive Form A and B subsets or as opposite ends of scatter points along a slope which traverses all points.

Much of the Pinto Creek and Phoenix data presented in this paper also represent a form of *a posteriori* analysis, inasmuch as we have partitioned *Corbicula* populations into Form A and B morphotypes prior to analysis. Whenever possible, however, we have utilized the entire sample for analyses; any intermediates were always assigned to either Form A or B categories. Thus, except for the data presented in Table 1 (sample size was restricted because of analysis constraints) and the reproductive survey (which required sectioning of relatively small numbers of individuals selected by size criteria), the original random sample can be restored by combining Form A and B subpopulations.

For example, specimens from Pinto Creek demonstrate the degree of overlap between Form A and B morphotypes. On December 19, 1982, a sample of 398 *Corbicula* collected from Pinto Creek at U.S. Highway 277, Kinney Co., Texas (locality N, Fig. 5), were categorized as either Form A (N = 204) or B (N = 194), with no intermediate phenotypes discarded. On the same date, additional Form B specimens (N = 145) were collected from locality I (Fig. 5). (Almost all of the specimens at locality I are Form B; see below.) These specimens provided the basis for the Pinto Creek data summarized in Fig. 3. When examined in the form of frequency distributions of basic shell ratios (Fig. 4) instead of mean ratios (Fig. 3), a markedly different picture emerges. Considerable overlap is evident between the subjectively determined groups. Differences are more apparent between the sympatric populations of Forms A and B (at Highway 277) than between the monomorphic population of Form B and either Form A or B in sympatric distribution. This could be construed as a reflection of absolute size differences between populations at the two localities, for the monomorphic population tends to have larger individuals than those from the Highway 277 area. However, ratio values are poorly correlated with size dimensions (the highest correlation, r = 0.46, was calculated for the length vs height/length comparison for locality N specimens). Although sulcation spacing appears to be a function of size among Form A and B morphotypes (Fig. 2), basic shell ratios seem to vary among populations independent of specimen size, at least within the length range of 5 to 30 mm. We can conclude from these observations that sympatric populations of Form A and B morphotypes may display a considerably greater degree of overlap of basic shell dimensions than is evident in either figs. 1 and 2 of Hillis & Patton (1982) or in our Fig. 3.

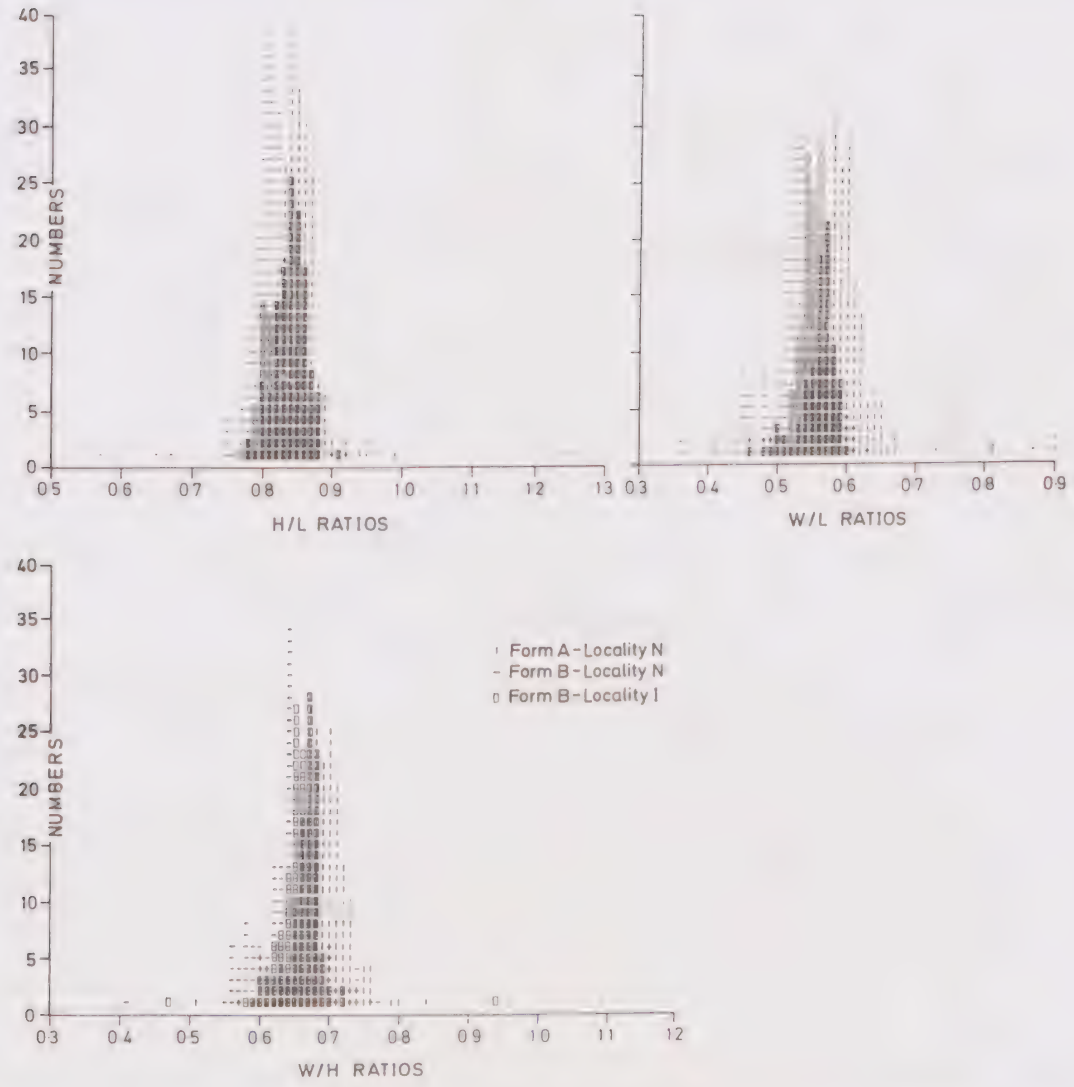

FIG. 4. Frequency histograms of basic shell dimension ratios (height/length, width/length and width/height) of samples of *Corbicula fluminea* collected December 19, 1982, from localities I and N (Fig. 5), Pinto Creek, Kinney Co., Texas. The abscissa represents the basic dimension ratio; the ordinate represents the number of individuals found to express a specific ratio value. All specimens from locality I (open box, N = 145) are Form B morphotypes. Specimens from locality N were determined to be either Form A (vertical line, N = 204) or Form B (horizontal line, N = 194); no intermediate phenotypes were discarded.

In contrast, the analysis of potential differences between subjectively determined similar and different morphotypes adds an additional dimension to the problem. When mean values of basic dimension ratios determined from samples collected at all localities are compared, a strikingly high proportion of differences between populations is encountered. Analyses of variance among Form A, Form B and combined Form A and B populations indicate statistically significant added variance components for all comparisons; however, these analyses all suffer from heteroscedasticity. The alternate comparisons between pairs of arcsin transformed mean height/length, width/length and width/height ratios using the approximate test of equality of means with heterogeneous variances also demonstrate a very high proportion of statistically significant differences ($p < 0.05$) between populations (Table 1). Within most populations, the basic dimension ratios and their arcsin transformed values have remarkably low variability (as indicated by standard deviations, Table 1). In fact, variability seems sufficiently

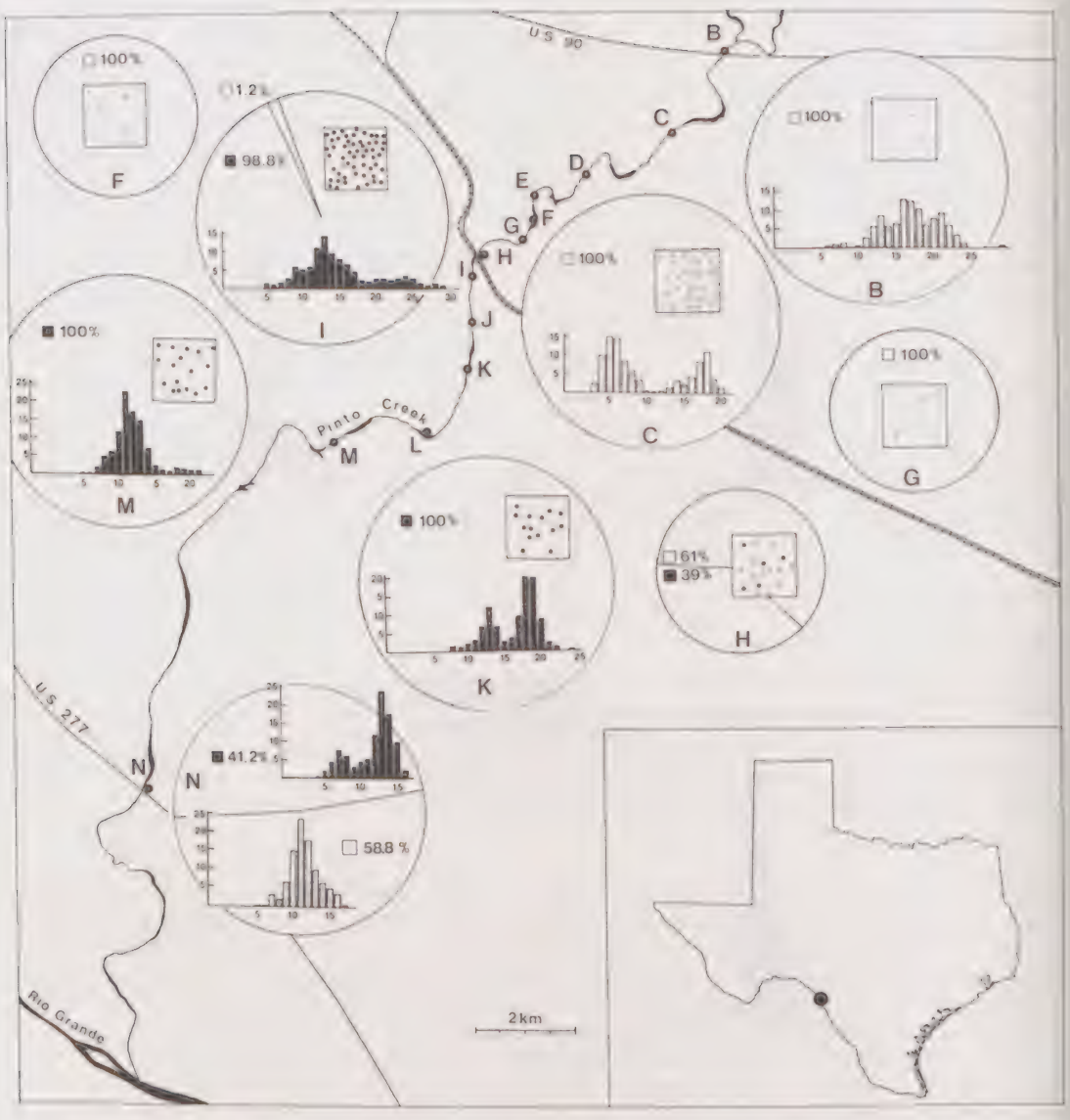

FIG. 5. Pinto Creek, Kinney Co., Texas, from U.S. Highway 90 to the Rio Grande River. Letters indicate specific sampling localities; sampling dates are given in Table 3. The large circles present additional data for Form A (open circles, squares or bars) and B (closed circles, squares or bars) morphotypes at the indicated localities. The circle is divided according to percent frequency of occurrence for each morphotype, and these percents are indicated for each circle. Squares within each circle illustrate the mean density of *Corbicula* per m^2 and the relative abundance of Form A (open dots) and Form B (closed dots) morphotypes. Length-frequency histograms for samples of Form A and/or B morphotypes also are illustrated. The abscissa represents length in mm; the ordinate represents the number of animals of a given size expressed as a percentage of the total sample. Collections from which density diagrams or length-frequency histograms were constructed were made on December 19, 1982, for localities I and N; on January 29, 1982, for localities B, C and G; and on March 4, 1983, for localities H, K and M. Additional information for each locality appears in the text and Table 3.

slight within each population that one might argue that many individuals within the population were cloned. (We contend that self-fertilization is an important consideration in understanding *Corbicula* polymorphism and population dynamics and we will return to this point later.)

There are more differences between populations with respect to the arcsin transformed ratios than similarities among them (Table 1). This should be expected when Form A (+ Hong Kong light) populations are compared with Form B (+ Hong Kong dark) populations. Of 108 comparisons of this type, 83% of the paired comparisons between means indicate a statistically significant difference ($p < 0.05$).

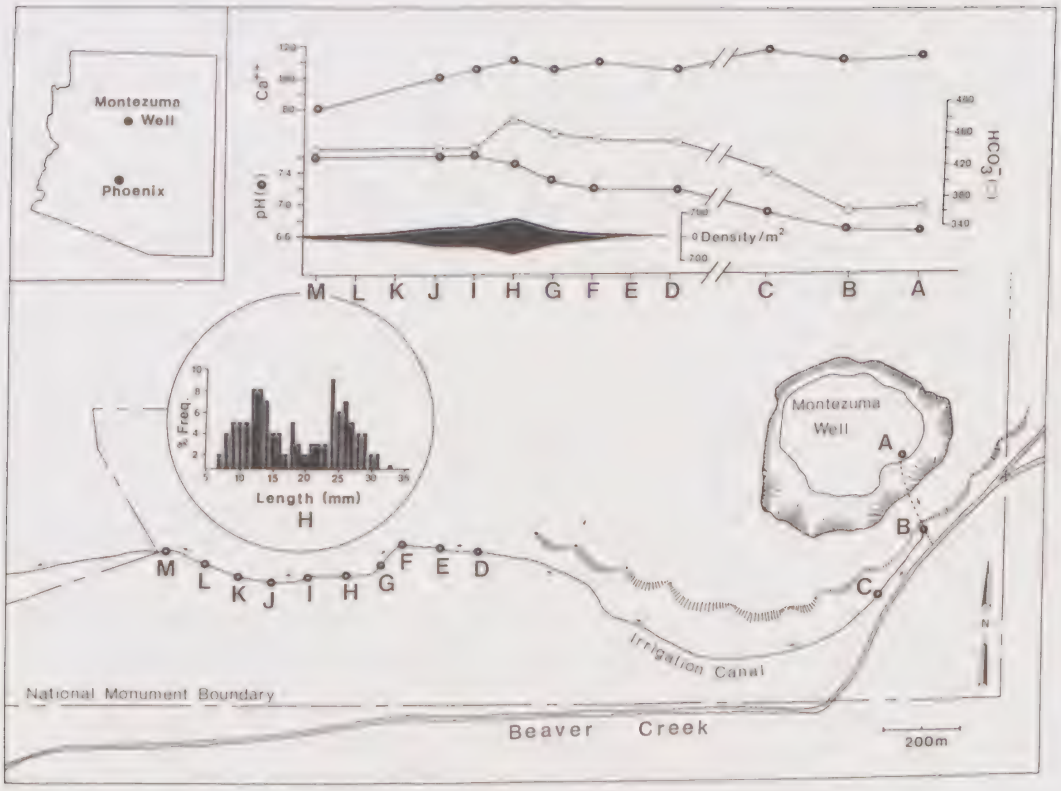

FIG. 6. Montezuma Well National Monument, Coconino Co., Arizona, and the associated irrigation canal. Letters indicate specific sampling localities; sampling dates are given in Table 2. *Corbicula* populations consist exclusively of Form B morphotype. A length-frequency histogram for *Corbicula* at locality H is given in the circle inset, where the abscissa represents shell length in mm and the ordinate represents the number of animals of a given length expressed as a percentage of the total sample. Relative density (individuals/m^2) determined in October 1982, prior to canal dewatering, and calcium ion concentration (Ca^{++} in mg/l), bicarbonate (HCO_3^- in mg/l) and pH (all determined in June 1983) are plotted according to each sampling locality. Calcium depletion (as travertine deposition) and concurrent increases in pH and bicarbonate become more pronounced toward the end of the warm season (Cole & Batchelder, 1969).

Intra-morph comparisons, however, also demonstrate a surprisingly high percentage of statistically significant differences. When Form A (+ Hong Kong light) populations are compared, 49% of the 45 mean pairs are significantly different; whereas when Form B (+ Hong Kong dark) populations are compared, 53% of the 45 comparisons also are significantly different.

Several alternative conclusions are possible with these data. First, one might conclude that all morph populations differing by one or more mean shell dimensions might represent separate species. Few would accept this hypothesis, for this would mean that as many as 10 separate species (one for each locality studied here) occur in the United States. If the first hypothesis is rejected, then there is a strong case for a single species, and a relatively weak case for a two-species model, according to these data. In fact, the Hillis & Patton (1982) morphometric data represent only a subset of the more general case tested here. In that light, their morphometric analysis simply demonstrates that, in a single locality, preselected shell criteria can be shown to be statistically different, just as we have done with sympatric and allopatric populations from a much broader geographic area. But our data do not rely entirely upon differences over large distances, for some of the Phoenix Country Club samples are separated by less than 50 m (PCC-A1 and PCC-A2 with PCC-MX, Table 1), and two data sets (PCC-A1 and PCC-A2, Table 1) demonstrate a significant difference with respect to the width/length ratio for the same morphotype collected at the same locality at different seasons! Finally, if Form A and B morphotypes represent distinctly different species populations, one should expect fewer differences among intra-morph comparisons. This is not the case. Thus, the data support more strongly the concept of a range of variation within a geographically (= environmentally?) variable single species which, at any

TABLE 1. Shell ratio comparisons for several *Corbicula* populations from North America and Asia. Ratio data arcsin transformed prior to analysis. Data arranged according to increasing mean height/length ratios, with data for other ratios presented below the former.

Locality	N / length range (mm)	Ratio	Mean Ratio	s.d.	Mean Arcsin Transf.	s.d.	Differences MZW(B)	Differences PCC-A1(B)
MZW(B)	50 / 10 - 30	H/L	0.76	0.03	61.00	2.02	- - -	1.89
		W/L	0.52	0.02	46.05	1.14	- - -	1.69
		W/H	0.68	0.03	55.30	1.83	- - -	2.30
PCC-A1(B)	30 / 5 - 15	H/L	0.78	0.01	62.38	1.96	1.38	- - -
		W/L	0.47	0.04	43.55	2.22	*2.50	- - -
		W/H	0.61	0.05	51.12	2.87	*4.38	- - -
PCC-A2(B)	30 / 10 - 19	H/L	0.81	0.03	64.33	1.95	3.33	1.95
		W/L	0.52	0.03	46.25	1.85	0.20	*2.70
		W/H	0.64	0.02	53.29	1.49	*2.21	2.17
PC-M(B)	100 / 5 - 17	H/L	0.81	0.05	64.38	2.40	3.38	*2.00
		W/L	0.53	0.06	45.95	2.49	0.10	*2.40
		W/H	0.65	0.07	52.91	2.52	*2.59	1.79
HK(dark)	35 / 8 - 24	H/L	0.83	0.02	65.91	1.89	*4.91	*3.53
		W/L	0.51	0.03	45.46	1.62	0.49	1.91
		W/H	0.61	0.02	51.35	1.24	*4.15	1.79
PC-I(B)	100 / 9 - 28	H/L	0.84	0.03	66.13	2.00	*5.13	*3.75
		W/L	0.56	0.03	48.33	2.18	*2.48	*4.98
		W/H	0.66	0.04	55.09	2.56	0.41	0.23
PCC-D(A)	56 / 14 - 21	H/L	0.85	0.03	67.45	1.42	*6.45	*5.07
		W/L	0.61	0.02	51.29	1.34	*5.24	*7.74
		W/H	0.71	0.02	57.69	1.31	*2.19	*3.97
PCC-MX(A)	90 / 6 - 20	H/L	0.85	0.02	67.45	1.68	*6.45	*5.07
		W/L	0.59	0.02	49.91	1.26	*3.86	*6.36
		W/H	0.69	0.02	55.96	1.30	0.46	*6.57
PC-N(A)	100 / 6 - 19	H/L	0.85	0.03	67.71	2.31	*6.71	*5.33
		W/L	0.59	0.04	50.04	2.19	*3.99	*6.49
		W/H	0.69	0.04	55.98	2.36	0.48	*4.96
HK(light)	50 / 5 - 17	H/L	0.87	0.05	69.09	3.44	*8.09	*6.71
		W/L	0.57	0.04	49.04	2.10	*2.99	*5.49
		W/H	0.66	0.03	54.05	1.65	1.45	*2.93
PCC-C(A)	72 / 6 - 17	H/L	0.88	0.02	70.14	3.08	*9.14	*7.76
		W/L	0.59	0.03	49.99	1.76	*3.94	*6.44
		W/H	0.67	0.03	54.69	2.39	0.81	*3.57
BRAZ(A)	50 / 18 - 32	H/L	0.91	0.02	72.44	2.18	*11.44	*10.06
		W/L	0.64	0.03	52.87	1.85	*6.82	*9.32
		W/H	0.70	0.03	56.79	1.66	1.29	*5.67

MZW(B): Form B, Montezuma Well irrigation canal, October, 1982
PCC-A1(B): Form B, Phoenix Country Club, Locality A (Fig. 7), June, 1983
PCC-A2(B): Form B, Phoenix Country Club, Locality A (Fig. 7), October, 1983
PC-N(B): Form B, Pinto Creek, Texas, Locality N (Fig. 5), January, 1983
HK(dark): Dark form, from Hong Kong irrigation furrows, April, 1983
PC-I(B): Form B, Pinto Creek, Texas, Locality I (Fig. 5), January, 1983

(*) indicates rejection of the null hypothesis ($p < .05$)

TABLE 1. (Continued)

between means (lower half) and minimum significant differences (upper half) for pairs of means

PCC-A2(B)	PC-N(B)	HK(dark)	PC-I(B)	PCC-D(A)	PCC-MX(A)	PC-N(A)	HK(Light)	PCC-C(A)	BRAZ(A)
4.80	4.72	2.05	1.66	1.63	1.60	1.74	2.69	2.18	2.00
1.83	1.39	1.53	1.27	1.14	0.99	1.27	1.62	1.34	1.47
1.80	1.70	1.59	1.70	1.49	1.40	1.65	1.66	1.80	1.66
2.17	1.73	2.02	1.62	1.60	1.57	1.90	2.68	2.15	2.10
2.21	1.89	1.98	1.82	1.73	1.63	1.82	2.05	1.79	1.94
2.34	2.27	2.19	2.28	2.12	2.06	2.34	2.24	2.35	2.24
- - -	2.10	2.30	1.98	1.96	1.94	2.05	2.88	2.43	2.26
- - -	2.01	2.09	0.94	1.86	1.78	1.94	2.16	1.92	2.05
- - -	1.77	1.68	1.78	1.57	1.49	1.72	1.72	1.87	1.72
0.05	- - -	1.91	1.44	1.43	1.38	1.54	2.60	2.04	1.85
0.30	- - -	1.76	1.53	1.43	1.32	1.53	1.83	1.50	1.70
0.38	- - -	1.55	1.66	1.43	1.34	1.60	1.61	1.76	1.61
1.58	1.53	- - -	1.81	1.79	1.76	1.89	2.78	2.29	2.12
0.79	0.49	- - -	1.67	1.57	1.48	1.68	1.93	1.65	1.81
1.94	*1.56	- - -	1.56	1.31	1.20	1.49	1.30	1.66	1.50
1.80	*1.75	0.22	- - -	1.29	1.23	1.41	2.52	1.98	1.75
*2.28	*2.58	*3.07	- - -	1.31	1.80	1.42	1.75	1.39	1.61
*1.80	*2.18	*3.74	- - -	1.45	1.35	1.61	1.62	1.77	1.63
*3.12	*3.07	1.54	*1.32	- - -	1.22	1.39	2.51	1.94	1.73
*5.04	*5.34	*5.83	*2.76	- - -	1.05	1.25	1.66	1.29	1.51
*4.40	*4.78	*6.34	*2.60	- - -	1.05	1.37	1.39	1.57	1.39
*3.12	*3.07	1.54	*1.32	0.00	- - -	1.34	2.48	1.91	1.69
*3.66	*3.98	*4.45	1.38	*1.38	- - -	1.18	1.56	1.16	1.40
*2.67	*3.05	*4.61	0.87	*1.73	- - -	1.27	1.29	1.48	1.30
*3.38	*3.33	1.80	*1.58	0.26	0.26	- - -	2.57	2.02	1.83
*3.79	*4.09	*4.58	*1.51	1.25	0.13	- - -	1.74	1.39	1.61
*2.69	*3.07	*4.63	0.89	*1.71	0.02	- - -	1.56	1.71	1.56
*4.76	*4.71	*3.18	*2.96	1.64	1.64	1.38	- - -	2.88	2.73
*2.79	*3.09	*3.58	0.51	*2.25	0.87	1.00	- - -	1.72	1.58
0.76	1.14	*2.70	1.04	*3.64	*1.91	*1.93	- - -	1.72	1.57
*5.81	*5.76	*4.23	*4.01	*2.69	*2.69	*2.43	*1.05	- - -	2.25
*3.74	*4.04	*4.53	1.46	1.29	0.08	0.05	0.95	- - -	1.58
1.40	*1.78	*3.34	0.40	*3.00	1.27	1.29	0.64	- - -	1.73
*8.11	*8.06	*6.53	*6.31	*4.99	*4.99	*4.73	*3.35	*2.30	- - -
*6.62	*6.92	*7.41	*4.34	*1.58	*2.96	*2.83	*3.83	*2.88	- - -
*3.30	*3.88	*5.44	*1.70	0.90	0.83	0.81	*2.74	*2.10	- - -

PCC-D(A): Form A, Phoenix Country Club, Locality D (Fig. 7), June, 1983
PCC-MX(A): Form A, Phoenix Country Club, 20 m downstream from well & canal water mixing point between Localities A & B (Fig. 7), June, 1983
PC-N(A): Form A, Pinto Creek, Texas, Locality N (Fig. 5), January, 1983
HK(light): Light form from Hong Kong irrigation furrows, April 1983
PCC-B(A): Form A, Phoenix Country Club, Locality B (Fig. 7), June 1983
BRAZ(A): Form A, Brazos River, Texas, January, 1982

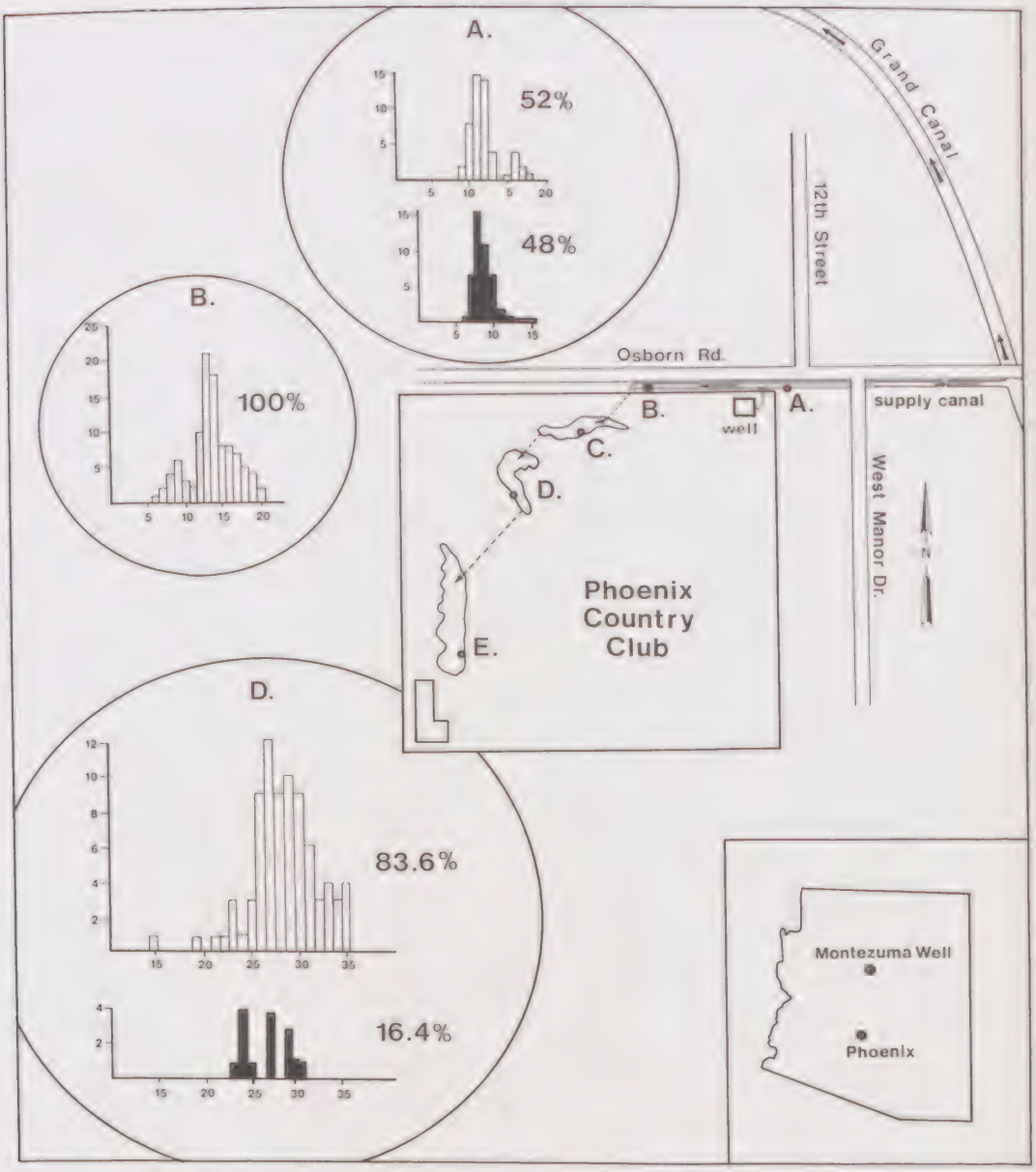

FIG. 7. The Phoenix Country Club, Phoenix, Maricopa Co., Arizona. Letters indicate primary sampling localities; additional supplementary *Corbicula* samples (some reported herein) were taken at approximately 50 m intervals between localities A and B (a total distance of about 250 m). Circle insets indicate the percent frequency of occurrence of Form A and B morphotypes and provide length-frequency histograms of Form A (open bars) and Form B (closed bars). The abscissa represents length in mm; the ordinate represents the number of animals of a given length expressed as a percentage of the total sample. Irregular shapes within the Phoenix Country Club grounds are ponds; the L-shaped structure in the lower left represents the clubhouse area. The figure is diagrammatic; distances are not to scale.

specific locality and at a specific time, may be only modestly variable. (The seeming differences between coexisting or "sympatric" Form A and B populations can and will be explained below.) Inasmuch as some of the populations compared are separated from one another by only a few meters of distance along a common stream system (the Phoenix Country Club populations), environmental rather than geographic criteria may be responsible for morphologic variation and are deserving of investigation.

THE HABITATS AND DISTRIBUTION OF NORTH AMERICAN *CORBICULA*

Form A habitats

Virtually all the present ecological literature on North American *Corbicula* refers to the Form A morphotype (e.g., Heinsohn, 1958; Sinclair & Isom, 1963; Abbott, 1979; Britton & Morton, 1979; Eng, 1979; Sickle, 1979; and many others). We will not review the literature here, except to point out that Form A is an opportunistic, eurytopic species successfully colonizing both lotic and lentic systems. For reference, we have examined a habitat occupied exclusively by the Form A morphotype: the Brazos River below DeCordova Bend Dam, Sommerville Co., Texas.

The Brazos River locality is just south of the Hood-Sommerville County line, approximately 30 river km downstream from the DeCordova Bend Dam, near Granbury, Texas. Here, the river flows over a bed of Cretaceous limestones which influence water quality. the pH of surface water ranges between 7.8 and 8.2. Specific conductance is high, generally above 2000 μmhos, with sodium, calcium, chlorides, sulfates and carbonates being the dominant ionic components. During periods of low discharge from Lake Granbury, surface flow at the study site is generally less than 0.4 m/sec; whereas, when floodgates are fully opened, surface flow may exceed 3 m/sec. There was never a time during the study period that this site experienced no flow. Water temperatures fluctuate seasonally (Fig. 8), with winter minima rarely below 0°C and summer maxima often in excess of 35°C.

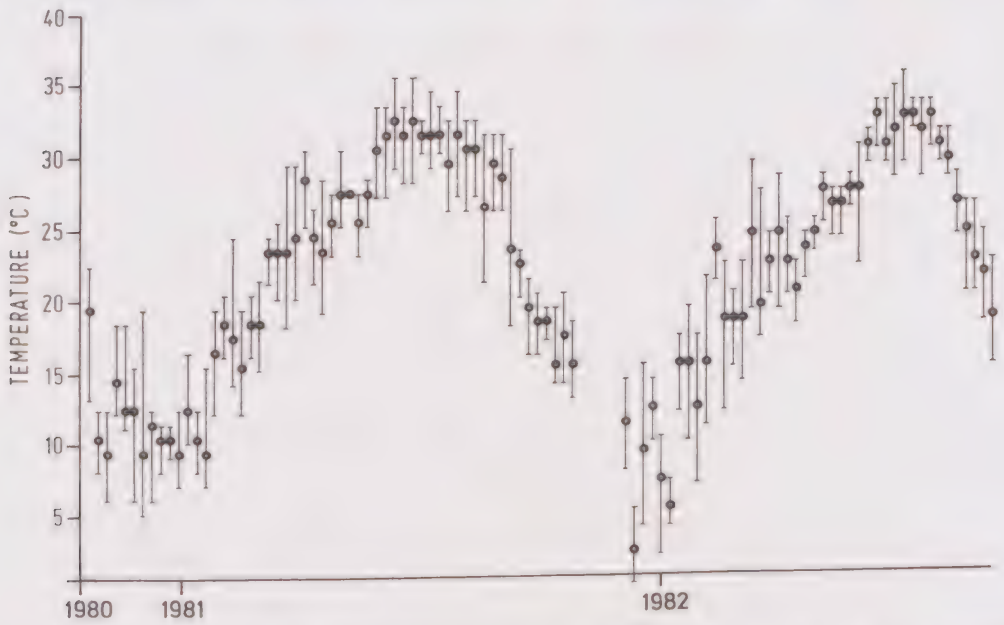

FIG. 8. Mean weekly water temperature (closed circles) for the Brazos River at Dennis, Texas, October 15, 1980, to September 30, 1982. Bars indicate maximum and minimum water temperatures recorded during the week. Data from the U.S. Geological Survey Water Resources Reports for 1980, 1981 and 1982.

Form B habitats

North American Form B seems to occur predominantly in permanent streams flowing through arid or semiarid portions of the southwestern United States (Fig. 1). Artesian streams of the Verde Valley, Arizona, are excellent examples of the microhabitat preferred by this morph.

The Verde Valley, Arizona

The Verde Valley lies between two arms of the Colorado Plateau in northcentral Arizona at elevations between about 900 m and 1250 m above sea level. The surrounding mountains are rich in porous limestones and carry a substantial load of groundwater to the carbonate-rich limestone bedrock on the valley floor. There are many permanent streams in the valley, most arising from artesian springs, seeps or sinkholes ("wells") that dot the surface. The streams flow many km through an otherwise

semiarid topography and most eventually return underground or evaporate from the desert sands to the south. Some of this water is now also diverted for agricultural irrigation.

Montezuma Well is a large (> 100 m diameter) sinkhole, which provides a constant source of artesian water to the upper Verde Valley via discharge to Beaver Creek and a small irrigation canal. The Well and its associated lotic tributaries have produced a number of endemic aquatic species (Polhemus, 1976; Cole & Watkins, 1977; Blinn et al., 1982) and provide a restricted microhabitat to which *Corbicula* has readily adapted.

The chemistry of Montezuma Well is unusual (Cole 1965; Cole & Batchelder, 1969; Cole & Barry, 1973; Brazel, 1976) (Table 2). It emerges from subterranean sources at a relatively low pH (typically < 7.0) and supercharged with calcium and bicarbonates. During the summer, groundwater enters the Well at a temperature of 24°C. Summer air temperatures frequently exceed 38°C; thus, water flowing from the Well is quickly heated, causing chemical precipitation of travertine. An estimated 88.8 kg $CaCO_3$/day is precipitated in the irrigation canal within 1.6 km of discharge, the majority being deposited within the lower 0.5 km (Cole & Batchelder, 1969). The pH of canal water fluctuates diurnally. During the day, it increases from less than 7.0 near the Well to almost 8.0 1.6 km downstream. A similar but less dramatic gradient persists at night.

TABLE 2. Montezuma Well and irrigation canal water chemistry.

LOCALITY (Fig. 6)	Ca++ (mg/1)	Mg++ (mg/1)	Na+ (mg/1)	K+ (mg/1)	pH	HCO3- (mg/1)	ALKALINITY (mg/1 CaCO3)	TEMP (C)
A								
Oct 82	58.80	18.20	25.20	3.90	—	—	—	—
Apr 83	108.00	26.70	36.00	—	6.7	330.00	484.00	22.5
Jun 83	115.00	27.20	41.00	—	6.7	350.00	440.00	24.0
B								
Oct 82	57.50	18.40	25.20	3.40	—	—	—	—
Apr 83	110.00	26.40	36.50	—	6.9	375.00	484.00	22.0
Jun 83	115.00	26.30	39.30	—	6.7	345.00	440.00	24.0
C								
Oct 82	—	—	—	—	—	—	—	—
Apr 83	118.00	26.70	36.60	—	7.0	390.00	482.00	22.0
Jun 83	119.00	27.50	41.80	—	6.9	390.00	440.00	24.0
D								
Oct 82	—	—	—	—	—	—	—	—
Apr 83	117.00	26.90	37.50	—	7.3	430.00	482.00	22.0
Jun 83	114.00	27.00	41.20	—	7.2	430.00	490.00	25.0
F								
Oct 82	60.50	18.30	25.20	3.90	—	—	—	—
Apr 83	115.00	26.50	36.80	—	7.4	430.00	479.00	22.0
Jun 83	115.00	26.70	40.30	—	7.2	430.00	490.00	25.0
G								
Oct 82	53.30	18.20	24.90	5.60	—	—	—	—
Apr 83	117.00	27.10	37.10	—	7.3	430.00	484.00	22.0
Jun 83	109.00	26.60	41.50	—	7.3	435.00	490.00	25.0
H								
Oct 82	52.80	18.10	24.80	4.60	—	—	—	—
Apr 83	117.00	27.20	36.10	—	7.5	450.00	482.00	22.5
Jun 83	116.00	27.20	42.00	—	7.5	460.00	490.00	25.0
I								
Oct 82	56.00	18.10	24.90	5.30	—	—	—	—
Apr 83	118.00	26.80	36.40	—	7.7	460.00	482.00	22.0
Jun 83	106.00	27.20	41.60	—	7.6	415.00	500.00	25.0
J								
Oct 82	—	—	—	—	—	—	—	—
Apr 83	120.00	25.80	37.70	—	7.7	460.00	482.00	22.0
Jun 83	98.00	27.00	40.90	—	7.6	418.00	505.00	25.0
K								
Oct 82	48.30	18.10	25.20	6.40	—	—	—	—
Apr 83	—	—	—	—	—	—	—	—
Jun 83	—	—	—	—	—	—	—	—
M								
Oct 82	37.00	18.30	23.90	5.30	—	—	—	—
Apr 83	113.00	26.30	37.90	—	7.9	457.00	473.00	22.0
Jun 83	79.00	22.60	42.60	2.84	7.6	420.00	510.00	25.0

Corbicula (Form B) has occurred in portions of the Montezuma Well irrigation canal since at least 1963 (National Park Service personnel, pers. comm.). It has never occurred in the well or in the upper ¾ km of the canal, being excluded in part by a small weir, but primarily by unsuitable water chemistry (Table 2). Maximum density of *Corbicula* occurs along that portion of the canal associated with highest travertine deposition. *Corbicula* disappears from the canal about 1.8 km downstream from Montezuma Well, where movable diversion locks periodically and alternately dewater the lower sections of the canal.

Form B *Corbicula* occur in numerous similar streams or irrigation canals throughout the Verde Valley, all of which are characterized by constantly flowing artesian source water, high travertine deposition and relatively low pH, which tends to increase downstream. Form A *Corbicula* do not occur in the Verde Valley, although they are common in the nearby Colorado River and throughout numerous irrigation canals and reservoirs in southern Arizona.

There is a remarkable correspondence between the physiography, water chemistry and distribution of Form B *Corbicula* in the Verde Valley of northcentral Arizona and Pinto Creek, Texas. Unlike the Verde Valley, however, both *Corbicula* morphs occur in portions of Pinto Creek, but only sometimes sympatrically.

Pinto Creek, Kinney County, Texas

Pinto Creek is a narrow, short (< 50 km), mostly constant flowing stream arising from artesian springs in northern Kinney County near the base of the Balcones Escarpement in southwestern Texas. It flows over limestone bedrock and fine caliche mud, occasionally passing underground, and eventually converging with the Rio Grande about 35 km downstream from Del Rio, Texas. The creek is supplied along its course by numerous seeps and springs (Brune, 1981), one of the most prominent being Stricklin Spring, which emerges near the middle portion of the creek (Fig. 5). In very dry years, surface flow along some portions of the creek dries, but groundwater flow and local springs provide a constant supply of standing water to the deeper pools.

Two major highways, two minor farm roads and one rail line cross the creek, providing ready access at several critical points along its course (Fig. 5). Texas Farm Road 2804 traverses the creek near its headwaters. *Corbicula* are absent at this locality. Form A *Corbicula* are present, however, 7.2 km downstream (Fig. 5, locality B) at the U.S. Highway 90 crossing. No distinctly Form B *Corbicula* are present here, although many specimens display a faintly to moderately bluish shell interior. This locality was collected on July 3, 1968, by Dwight Taylor and Jerry Landye, with no evidence of the presence of *Corbicula* at that time (J. Landye, pers. comm.). In 1982, living *Corbicula* occurred at this locality in densities of about 3-6/m^2. Form A attains the maximum density (about 20/m^2) in upper Pinto Creek about 2.6 km farther downstream (locality C). From here to Stricklin Spring (locality F), the density of Form A progressively decreases, due most likely to periodic interruptions of surface flow, especially in dry seasons. A few specimens survive beyond Stricklin Spring, where deep pools provide a refugia in times of drought.

An unpaved farm road (Texas 1572) and rail line cross Pinto Creek 10.5 km downstream from U.S. Highway 90. At this point, Form A *Corbicula* all but disappear, to be replaced by Form B at locality I. Within a very short distance downstream, Form B becomes the exclusive *Corbicula* morphology in the creek (localities, J, K, L and M). We were unable to obtain permission to sample along the 12 km of creek from localities M to N, but it is significant that three small dams or weirs are known to occur in this portion of the creek. At the U.S. Highway 277 crossing (locality N), both Forms A and B occur sympatrically, with the former almost twice as abundant as the latter. Only Form A has been reported from the Rio Grande (Metcalf, 1966; Murray, 1971; Metcalf & Smartt, 1972; Britton, 1982).

Winter water temperatures at Pinto Creek are slightly warmer than at the Brazos River locality, largely due to the mediating effects of the subtropical latitude (Fig. 9). Maximum air temperatures slightly exceed those at the Brazos, but summer water temperatures are tempered by cooled groundwater entering the creek from numerous springs and seeps. Otherwise, the water chemistry of Pinto Creek is similar to that of the Montezuma Well irrigation canal. Groundwater, high in calcium and carbonate ions and a relatively low pH, emerges at the springs. Downstream, pH values increase and calcium carbonate is chemically precipitated as travertine, especially during the warmer months (Fig. 15 and Table 3). Form B *Corbicula* also attain a maximum population density in Pinto Creek in a chemical environment similar to that of the Montezuma Well irrigation canal. As the chemical environment changes, so do the relative percentages of Forms A and B *Corbicula* in Pinto Creek. An even more dramatic example of this was found in Phoenix, Arizona.

TABLE 3. Water chemistry at Pinto Creek, Kinney Co., Texas.

LOCALITY (FIG. 5)	DATE	DISTANCE (km)	Ca++ (mg/1)	Mg++ (mg/1)	Na+ (mg/1)	K+ (mg/1)	TOTAL HARDNESS (mg/1)
A	3/04/83	0.0	75.20	2.93	27.20	0.94	199.80
B	12/20/82	7.2	84.10	4.25	38.80	1.22	227.50
	1/29/83		83.00	3.21	30.90	1.10	220.50
	3/04/83		82.30	3.25	32.40	0.75	218.90
C	1/29/83	9.8	76.00	3.08	30.30	1.20	202.50
D	1/29/83	11.1	64.20	2.99	30.80	1.20	172.60
E	1/29/83	15.3	58.60	3.06	31.10	1.10	158.90
	3/04/83		69.90	2.53	27.60	0.71	185.00
F	1/29/83	15.8	75.40	2.47	30.10	1.10	198.40
G	1/29/83	16.3	75.30	2.85	30.60	1.10	192.80
	3/04/83		69.60	2.65	30.20	0.71	184.50
H	3/04/83	17.8	90.90	2.92	33.20	0.72	229.90
I	12/19/82	18.3	83.60	4.08	41.50	1.30	225.60
	12/20/82		86.90	4.21	43.20	1.02	234.30
	1/29/83		88.40	3.07	30.00	1.20	233.40
	3/04/83		93.60	2.94	33.30	0.73	245.80
J	3/04/83	19.8	94.60	2.94	32.80	0.73	239.20
K	3/04/83	20.4	88.50	2.92	32.60	0.72	223.90
L	3/04/83	21.1	86.30	2.97	33.00	0.73	227.70
M	3/04/83	24.9	107.70	3.62	34.20	0.76	283.80
N	10/19/81	37.0					
	12/20/81						
	1/17/82						
	2/19/82						
	3/20/82						
	4/24/82						
	5/21/82						
	6/28/82						
	8/21/82						
	9/19/82		47.00	4.85	39.40	1.00	137.33
	11/06/82		75.50	4.98	48.30	1.32	
	12/19/82		84.40	5.12	43.40	1.22	231.80
	1/29/83		83.50	3.78	34.40	1.10	224.10
	3/04/83		72.10	3.91	36.00	0.64	183.90

TABLE 3. (Continued)

ALKALINITY pH 4.0 (mg/l)	WATER TEMP. (°C)	pH	DO (mg/l)	HCO_3^- (mg/l)	FREE CO_2 (mg/l)	$CO_3^=$ (mg/l)	TOTAL CO_2 (mg/l)
228.00	20.00	7.80	9.60	204.3	7.8	0.5	212.60
231.60	12.00	8.00		201.6	5.7	0.7	208.00
245.10	13.00	7.90	10.70	214.1	7.5	0.6	222.20
238.40	20.00	7.70		200.2	9.7	0.4	210.30
230.90	13.00	8.00	10.80	200.2	5.6	0.7	206.50
197.70	13.00	8.40	12.20	170.0	1.9	1.5	173.40
185.30	14.00	8.20	10.90	160.0	2.8	0.9	163.70
196.40	18.00	7.70		151.5	2.6	0.7	154.80
205.20	18.50	7.40	4.40	179.1	17.5	0.2	196.80
222.30	16.00	7.40	6.20	190.3	19.7	0.2	210.20
235.60		7.70		200.3	9.6	0.4	210.30
245.10	18.00	7.60	10.40	208.4	12.6	0.4	221.40
	16.00	7.50					
228.00	13.00	7.50		197.2	17.3	0.2	214.70
239.40	14.50	7.50	9.10	207.6	17.6	0.2	225.40
250.80	20.00	7.60	10.00	218.2	13.2	0.4	231.80
233.70		7.60		200.9	12.1	0.3	213.30
236.60	21.00	7.60	10.00	201.3	11.7	0.4	213.40
223.30	21.00	7.80	12.20	184.0	6.7	0.5	191.20
228.00	20.00	7.80	9.20	193.9	7.1	0.5	201.50
	22.00						
	11.00						
	9.50						
	16.00						
	18.00						
	23.00						
	29.00						
	29.00						
	30.00						
148.20	26.00	8.10		128.2	2.7	0.4	131.30
171.00	16.00	8.20		148.5	2.4	0.9	151.80
178.10	11.00	8.00		155.1	4.5	0.1	159.70
173.90	10.00	7.60	9.40	150.6	11.2	0.2	162.00
167.80	19.00	8.10	9.20	142.9	3.5	0.5	146.90

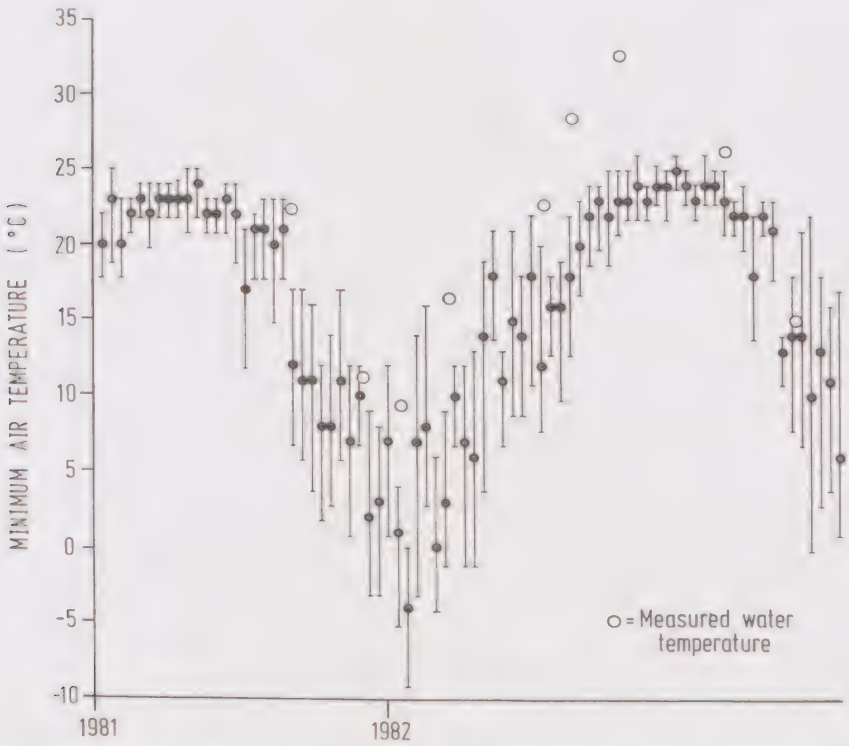

FIG. 9. Mean minimum weekly air temperatures (closed circles) recorded for Del Rio, Texas, from June 1, 1981, to November 30, 1982. Bars indicate maximum and minimum values of minimum air temperatures recorded for the week (U.S. Weather Service, Del Rio, Texas). Open circles indicate water temperatures recorded for Pinto Creek locality N (Fig. 5) during sampling periods (see Table 3).

Phoenix County Club

We investigated waters on and entering the grounds of the Phoenix Country Club in June and October 1983, initially to determine if they still contained polymorphic *Corbicula* as reported by Sinclair & Isom (1963). We found both Form A and Form B morphs in these waters distributed in a most interesting manner.

The Phoenix Country Club (Fig. 7) receives water for its golf course grounds and ponds from two sources: (1) an artesian well located near the northeast corner of the golf course, and (2) a canal, also entering from the northeast, delivering water from the Salt River. At Osborne and 12th streets, the alkalinity and total CO_2 of canal water was relatively low, possibly due to chemical precipitation upstream (Table 4). In contrast, the well water is high in alkalinity and total CO_2 (Table 4). Well water is delivered to and mixed with canal water about 20 m west of the intersection of Osborne and 12th streets outside the country club grounds. Mixed water flows westward in the canal and outside the golf course boundary fence for a distance of approximately 250 m, where it is then diverted southward to enter the golf course water distribution system. At the point of diversion and prior to entering the golf course boundary fence, water chemistry is only slightly different from that encountered upstream prior to mixing (Table 4). Thus, the canal receives a load of high alkalinity, high bicarbonate water at the point of well water mixing and dissipates the alkalinity and bicarbonates to almost ambient levels in a distance of no more than 250 m.

Both Form A and B *Corbicula* occur in the Salt River canal immediately prior to the point where this water mixes with well water (Fig. 7, locality A). Size-frequency distributions and numbers of individuals (A = 52%, B = 48%; N = 445) of each morph collected in June 1983 are very similar (Fig. 7, circle A). Form A *Corbicula* persist in the canal downstream from the point where river and well water mix, but Form B morphs disappear. All but five of 171 specimens collected in June 1983 at canal locality B (Fig. 7, 250 m downstream from the point of mixing) had a typical *C. fluminea* Form A shell morphology, including distinctly white or cream shell interiors. The five exceptions differed

TABLE 4. Water chemistry at Phoenix Country Club localities, June 27, 1983.

Water characteristics	Localities (Fig. 7)				
	Well	A	B	D	E
Temperature (°C)	24.50	24.00	24.00	27.00	29.00
pH	7.40	7.70	8.10	7.70	9.20
Total hardness (mg/l)	267.00	110.50	125.00	175.30	142.80
Alkalinity (mg/l $CaCO_3$)	252.00	115.00	130.00	165.00	142.50
Total CO_2 (mg/l)	231.60	110.00	127.10	158.00	131.50
Ca^{++} (mg/l)	58.10	29.90	32.90	40.20	23.70
Mg^{++} (mg/l)	29.60	8.70	10.40	18.20	20.30
Na^{+} (mg/l)	21.20	31.60	45.10	12.30	20.60
K^{+} (mg/l)	2.32	1.40	1.48	1.78	2.48

only by display of a faint purple blaze on the shell interior, but otherwise were insufficiently distinct to be identified as Form B. A very similar distribution was observed when the canal was revisited in October 1983. Thus, within a distance of no more than 250 m, the population structure had changed from approximately equal numbers of Form A and B morphotypes to the complete absence of one. As the only other apparently radical variation along this short distance is a striking change and recovery of water chemistry, it seems reasonable to conclude a cause and effect relationship between morphotype distribution and water chemistry. The question, of course, is whether the change in water chemistry acts primarily to bring about selective mortality, a phenotypic change, both, or neither in Form B *Corbicula*.

Sinclair & Isom (1963) reported a population of mixed *Corbicula* morphotypes in the Phoenix Country Club golf course ponds. In 1983, these ponds still supported a mixed population, although the relative frequency of Form B morphs is low (< 20%). Furthermore, the number of Form B specimens is highest in the pond nearest the water intake canal (near Fairway 12), and diminishes along the water distribution system. There are less than 5% Form B morphs in the pond near green 18 at the end of the water system. Furthermore, we found no juvenile *Corbicula* of either morphotype in any of the ponds. The pond populations do not appear to be reproducing, but are recruited from an external source. The only known source is the canal. Thus, some Form B specimens must survive the apparent chemical barrier at the point of well mixing or may be transmitted past it during periods when mixing does not occur. The *Corbicula* situation at the Phoenix Country Club is far from resolved, but it continues to support the possibility of environmental generation of phenotypic polymorphism.

POPULATION DYNAMICS AND SIZE-FREQUENCY DISTRIBUTIONS

The Brazos River

The length-frequency distribution of *Corbicula fluminea* (Form A) from the Brazos River (Fig. 10) is very similar to that described in previously published reports of *C. fluminea* population structure in Asia (Morton, 1977) and North America (Aldridge & McMahon, 1978; Eng, 1979; Sickel, 1979). *Corbicula fluminea* lives to a maximum of approximately three years in the Brazos River and reaches a maximum shell length of about 33 mm. In September 1981, four age groups occurred in the population: a large size class (28-32 mm) representing a 1979 generation, the dominant size class (18-27 mm) representing a 1980 generation, and two smaller size classes (11-16 and 5-10 mm) representing spring and fall 1981 generations, respectively. Throughout the sampling period, which includes a relatively dormant winter season, the 1980 generation remained dominant. The only survivors of the late spring 1982 flooding were also representatives of this size class.

Between September and October 1981, the numbers of fall juveniles increased significantly, suggesting a substantial spatfall between sampling periods. During the winter, none of the four generations represented in the population grew to any appreciable degree, a situation frequently observed in and apparently characteristic of populations of *Corbicula fluminea* from other localities (Morton, 1977; Eng, 1979). There was also a progressive mortality or loss of the fall 1981 generation from the samples,

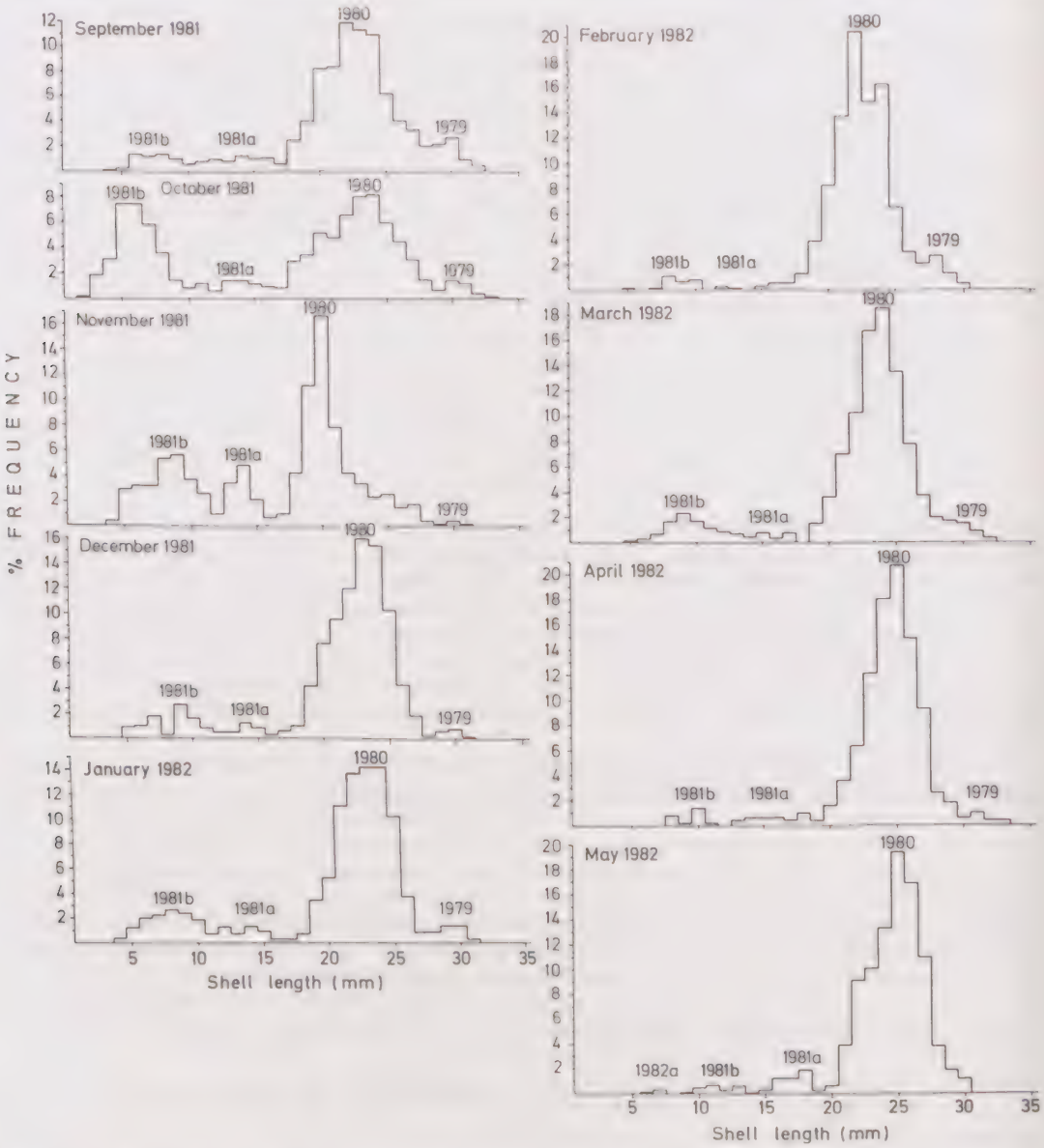

FIG. 10. Length-frequency histograms of samples of *Corbicula fluminea* Form A collected from September 1981 to May 1982 from the Brazos River approximately 30 river km downstream from the DeCordova Bend Dam near the Hood-Sommerville Co., Texas, boundary. Length in mm is represented on the abscissa; the number of animals at a specific length expressed as a percentage of the total sample is represented on the ordinate. The dates above individual peaks indicate the dates at which the particular size classes settled.

possibly in part the result of downstream transport during brief episodes of high water flow following release of water from Lake Granbury. In March and more obviously April 1982, all generations resumed growth (Fig. 11).

The spring 1982 generation emerged in May. A prolonged period of flooding then occurred during the early summer. When the locality again became accessible for sampling in August 1982, at least 90% of the population had been washed away or destroyed, including virtually all individuals below 20 mm shell length. Despite the unscheduled termination of population sampling from the Brazos locality, there are sufficient data to conclude that the population dynamics of Brazos River *Corbicula fluminea* are consistent with that observed for other populations. Thus, it is reasonable to assume

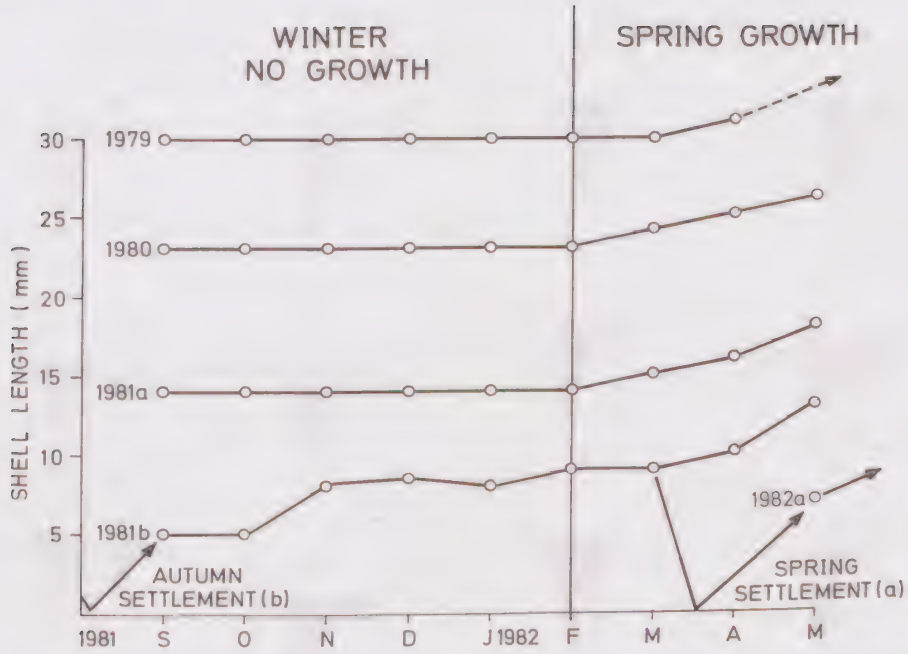

FIG. 11. The mean length of each size class in the monthly samples of *Corbicula fluminea* from the Brazos River, Texas, locality. The dates indicate the year of settlement of each age group. The winter period is marked by little to no growth, especially within the larger size classes. Growth resumes in the spring samples. The sampling program was terminated abruptly following the May sampling due to severe and prolonged flooding with concurrent loss of the *Corbicula* population at this locality.

that, if spring flooding had not been so severe, each generation surviving in May 1982 would show significant growth during the summer season and the 1980 generation would decline in numbers, being replaced by individuals of the 1981 generation.

In summary, there are two spatfalls per year in spring and autumn. These can be correlated with a progressive rise in water temperature (Fig. 8) from a mean winter low of approximately 10°C to a mean summer high of 32°C, during which time there is a spring settlement. The autumn settlement occurs as summer temperatures decline to winter minima. Little growth occurs in the population from November to February, but growth precedes the spring settlement of pediveligers.

Pinto Creek

Length-frequency histograms for Forms A and B *Corbicula* from the U.S. Highway 277 crossing at Pinto Creek (Fig. 5, N) are shown in Fig. 12. Form A is represented by light bars on top and Form B by dark bars on the bottom. This format permits direct visual comparisons between populations for each collecting period. Population structure for both morphs is more easily visualized, however, by plotting the average length of each generation for each of the sampling periods (Fig. 13).

At this locality, neither *Corbicula* morph survives more than about two years nor achieves a shell length in excess of about 25 mm. Most specimens have a shell length of less than 20 mm. This is in striking contrast to the Brazos River population, although Form A specimens at Pinto Creek are virtually indistinguishable from those in the Brazos River. It is unlikely that direct competition between morphs is responsible, for neither appears to have significantly increased survival at the expense of the other. More likely, one or more environmental factors are suboptimal, suggesting that this may be a marginal habitat for both morphs, with Form A being slightly better adapted than Form B. The Form A morph consistently attains a larger size than Form B. This is due in part to a slightly faster growth rate in the former (Fig. 13, February to July 1982), but also due to a slightly longer life span. The latter is indicated by the presence of the 1979 generation remnant in the September 1981 sample, and the consistent representation of the Form A 1980 generation from December 1981 to June 1982.

Growth dynamics for both Pinto Creek morphotypes are revealed in Figs. 12 and 13. September, October and November 1981 frequency histograms (Fig. 12) are difficult to interpret, due largely to

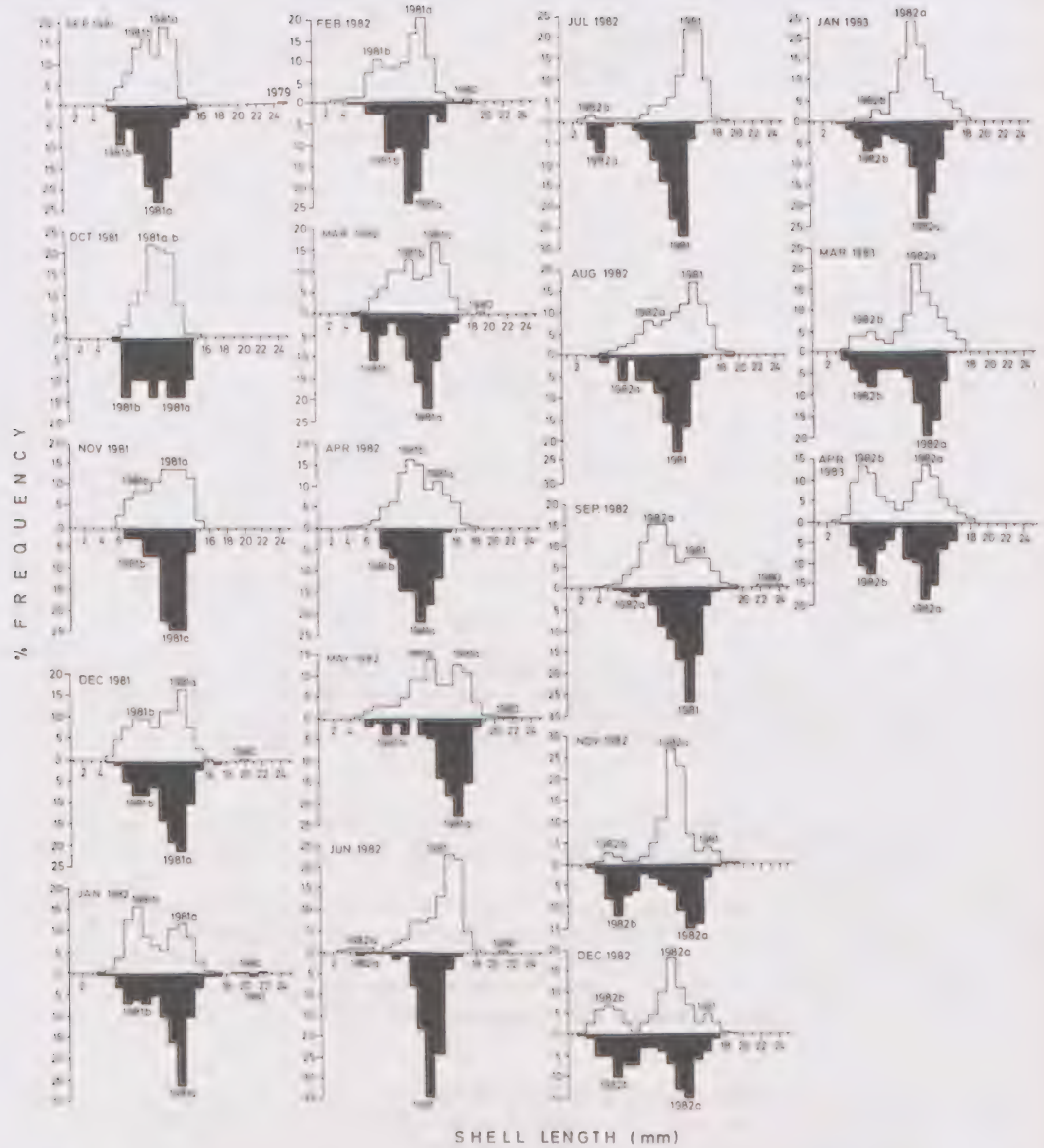

FIG. 12. Length-frequency histograms of samples of *Corbicula fluminea* collected from September 1981 to April 1983 from locality N (Fig. 5), Pinto Creek, Kinney Co., Texas. The upper (white) bars represent Form A morphotypes, whereas the lower (dark) bars represent Form B morphotypes. The abscissa represents shell length in mm; the ordinate represents the number of animals of a given length expressed as a percentage of the total morphotype sample. The dates above (Form A) or below (Form B) individual peaks represent the dates at which these particular age classes settled.

relatively small sample sizes. The large Form A specimens collected in September 1981 are clearly the remnants of a 1979 generation, but the 1980 population is not represented until December. The 1980 Form B population appears only once (January 1982), reinforcing the idea of a somewhat longer survival for the Form A morph.

In addition to the few 1980 Form A individuals, two distinct generations are apparent for both morphs beginning with the December 1981 sample. There is very little growth in either population from December to February 1982, followed by a period of spring growth from March to June. Form A grows faster than Form B, especially with respect to the smaller size class (fall 1981 generation).

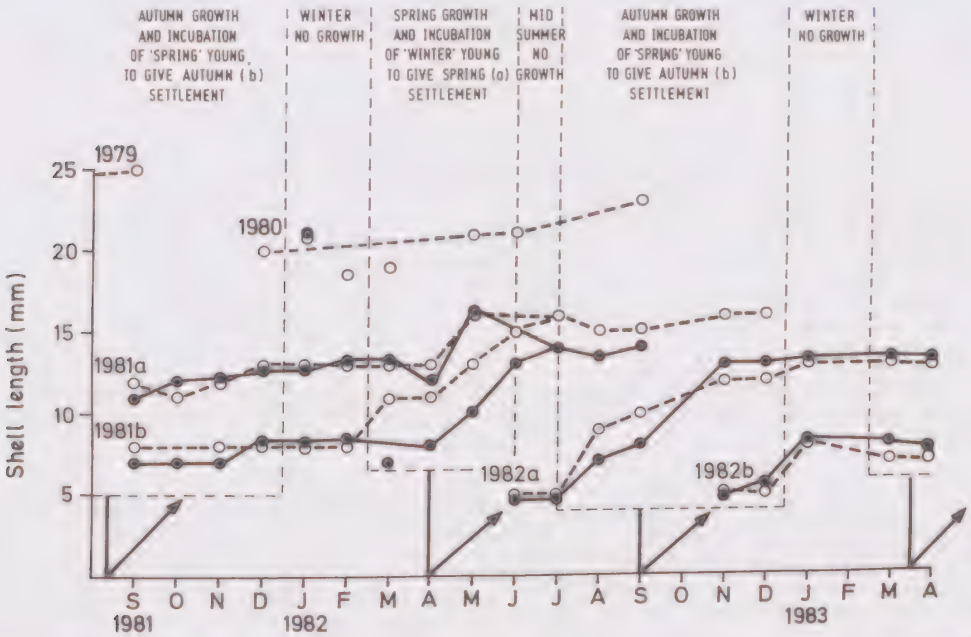

FIG. 13. The mean length of each age class in the monthly samples of Form A (open circles) and Form B (closed circles) *Corbicula fluminea* collected from locality N, Pinto Creek, Kinney Co., Texas. The dates indicate the year of settlement for each age group. Both populations are characterized by two spatfalls per year with juveniles entering the population in late spring and autumn, periods of growth quiescence during winter and mid-summer, and periods of relatively rapid growth during spring and autumn. The pattern of growth for both Form A and B morphotypes corresponds exactly with that observed for *C. fluminea* from Plover Cove, Hong Kong (Morton, 1977), and several North American populations (see text). Form A displays slightly more rapid spring and autumn growth than that observed for Form B at the same locality.

The spring 1982 generation emerges in the samples for both morphs in July, having been released in May or June (see reproductive survey, below). Both morphs pass through a period of little growth during mid-summer, with the 1981 generation also demonstrating little growth throughout the fall. The spring 1982 generation grows rapidly from July to November, with both morphs attaining lengths of 12 mm in six months and rapidly dominating succeeding samples, particularly Form B. In November, 1982 autumn juveniles of both morphs enter the sample.

Form B appears to survive no more than 18 months. Form A is more typical of the Brazos River *Corbicula fluminea* and can survive into its third year of life in this environment, although most individuals live less than two years. Despite the slightly accelerated growth rate and somewhat longer survival for Form A, there is a striking similarity of population structure for both morphs. In terms of population structure, there is little justification in recognizing subpopulations.

In summary, settlement and growth of both Pinto Creek morphs can be linked to seasonal changes in air and water temperature. Spatfalls occur in the spring and autumn during periods of rising or falling seasonal adjustments. No growth occurs in mid-winter or mid-summer when temperatures are extreme. Spring and autumn are also periods of growth and incubation of fertilized eggs, the latter being released toward the end of each growth period. All of these observations correspond well with the pattern observed in *Corbicula fluminea* from the Brazos River and other localities.

The frequency of occurrence of Form B at Pinto Creek locality N is variable (Fig. 14). In September 1981, it accounted for 23% of the total population, but fell to 15% in October. Thereafter, Form B rose to a maximum of 21% in December and then progressively fell to a minimum of 8% in April. Subsequently, the incidence of Form B rose to a peak of almost 50% in January 1983 and then fell again. The fluctuating frequency of Form B could in part be related to stream transport from monomorphic upstream populations, especially following the heavy flooding which occurred in May 1982, and again in October and November 1982 (Fig. 14). It is also possible that the high incidence of Form B in December/January 1982 and January 1983 represents greater survivorship of previous spring Form B spatfalls. Aldridge & McMahon (1978) have shown that the spring spatfall is the more

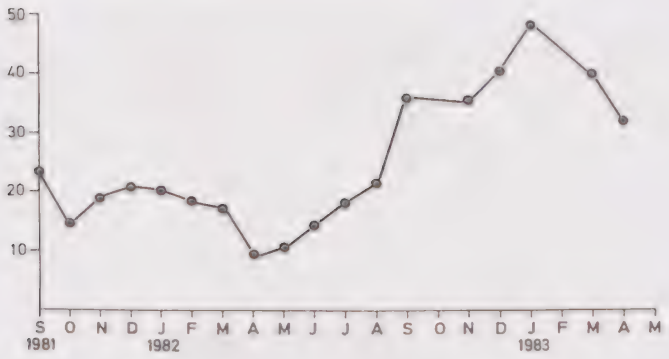

FIG. 14. The percent frequency of Form B morphotypes at locality N, Pinto Creek, Kinney Co., Texas. The abscissa represents monthly sampling periods and the ordinate represents the percent occurrence of Form B in each monthly sample.

important in *Corbicula fluminea* in the United States. Hermaphroditic, probably self-fertilizing (see below) Form B may be able to have a greater reproductive success in a spring spatfall, and a slightly higher survivorship during critical summer stress periods (being largely restricted in geographic distribution to typically spring-fed constant-flowing streams in arid climates), effectively increasing the relative frequency of the Form B morph the following winter. Form A perhaps has a selective advantage during the autumn spatfall. The moderation of temperature stress in the winter could be detrimental to Form B and selectively advantageous for Form A juveniles. There also may be environmental selection upon developmental or juvenile stages which may influence the phenotypic characteristics of either or both morphotypes. It is possible that the fluctuating environment could induce Form A phenotypes in Form B juveniles and *vice versa* (see below).

The incidence of one morph over the other varies not only in time at one locality but also down the length of the creek as hydrological parameters change with fluctuations in the flow of source water. Size-frequency distributions for *Corbicula* were made from December 1982 to March 1983 at several Pinto Creek localities (Fig. 5). As *Corbicula* grow little in winter, frequency distributions made on different dates during this time are more reliably compared than if they were made at different times during other seasons.

Corbicula attains significantly larger sizes and hence has longer survivorship in Pinto Creek localities having only monomorphic populations. At least three size classes occur at the U.S. Highway 90 crossing (Fig. 5, B), where only Form A is present. The 20-25 mm size class is a major component of the population here, unlike the situation at the U.S. Highway 277 crossing. At locality C, 2.6 km downstream, the population remains monomorphic Form A, but the size-frequency distribution is distinctly bimodal, with the 15-20 mm size class a significant component of the population. Both morphs occur at the U.S. Highway 277 crossing (locality N). Here, the Form A frequency distribution, collected in January 1983, is slightly bimodal, with no specimens larger than 18 mm.

Form B was the sole morphotype at two localities where frequency distributions were made (localities K and M) and overwhelmingly dominant at a third (locality I). In all of these localities, frequency distributions were at least bimodal. At locality I, specimens reached a maximum size of 30 mm, with a distinct mode at about 24 mm. Maximum shell length progressively decreases downstream from locality I, with 25 mm and 21 mm being the largest specimens at localities K and M respectively. In all these localities, however, Form B grows significantly larger than at the U.S. Highway 277 crossing, where maximum shell length was 16 mm in January 1983. The progressively decreasing maximum shell length of Form B *Corbicula* from locality I to M, combined with the changing water chemistry along this portion of the creek suggests environmental conditions may be responsible (Fig. 15).

The distribution of morphotypes down Pinto Creek can be correlated with changes in water quality (Fig. 15). At localities A-H, only Form A occurs. Between localities H-M, only Form B occurs, while at the lowest locality (N), both occur. The change in incidence of the populations occurs as water quality changes along the stream. Above localities E and F, a spring (Stricklin Spring) emerges to mingle with the stream water. There is an immediate increase in CO_2 (as $-HCO_3$) and Ca^{++}, and a sharp decrease in pH. Downstream from this locality smaller springs continue to enter the creek, causing the altered water chemistry to persist at least to locality M. Somewhere between M and N, the

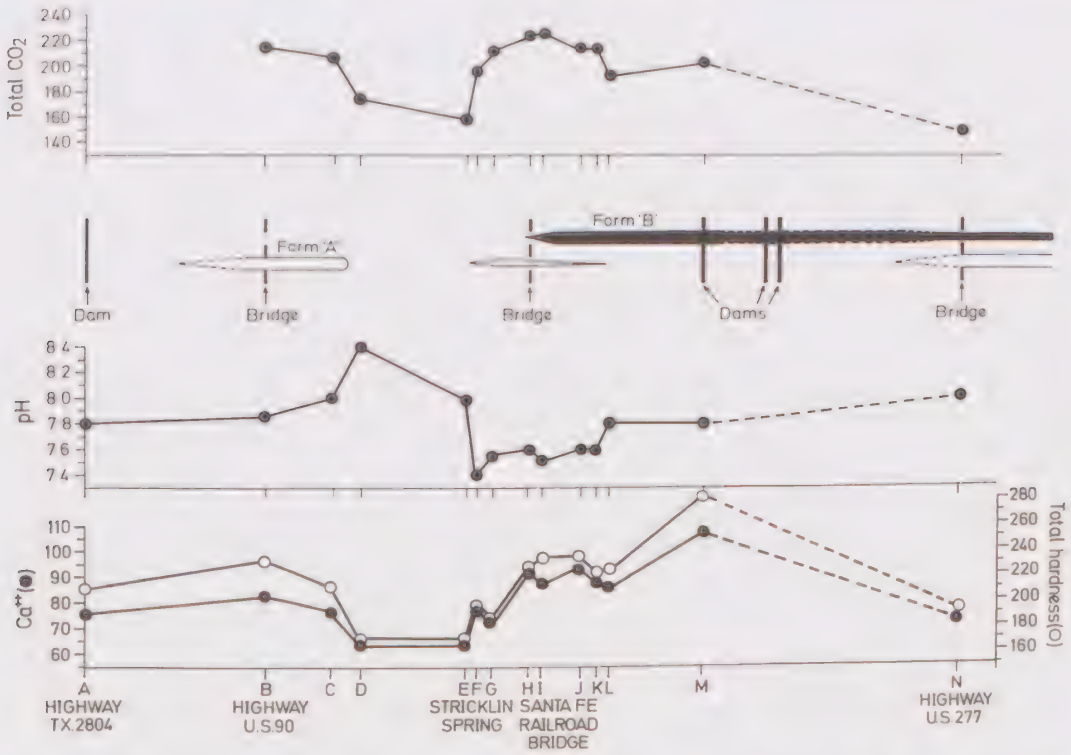

FIG. 15. Water chemistry and the distribution of *Corbicula* morphotypes in Pinto Creek, Kinney Co., Texas. Letters along the abscissa represent collecting localities (see Fig. 5), with distances between localities (Table 3) approximately to scale. Calcium, total hardness and total CO_2 are reported as mg/l. The relative abundance of Form A (light bars) and B (dark bar) morphotypes is illustrated above the pH plot. The locations of known bridges and dams across Pinto Creek are shown in this figure. Dashed lines indicate unsampled and hence inferred distributions. See text for additional information on specific localities.

importance of artesian water declines. The occurrence of Form B is directly correlated with low pH and high CO_2/Ca^{++}. An exactly comparable water chemistry is found at the Montezuma Well irrigation canal (Cole & Batchelder, 1969), where only Form B *Corbicula* occur, and a similar (though not precisely comparable) situation is also seen at the Phoenix Country Club. It appears to be more than coincidence that this specific water chemistry is associated with the occurrence of the Form B morphotype.

SEXUALITY

The Brazos River

Brazos River *Corbicula* (exclusively Form A) mature quickly, with developing gametes present in most individuals attaining a shell length of 8 mm (Table 5 and Fig. 16A). The riverine specimens (N = 167) mature into females (41.3%) or hermaphrodites (58.7%). Larvae are incubated in spring (April-May) and fall (September-November). Thus, the pattern of sexuality of *C. fluminea* in the Brazos River is similar to the pattern established for the species at numerous lotic localities in North America (Heinsohn, 1958; Sinclair & Isom, 1963; Kraemer & Lott, 1977; Kraemer, 1979) and Asia (Morton, 1977; 1983).

Montezuma Well irrigation canal

This population of Form B *Corbicula fluminea* was sampled only once (October 21, 1982) to determine sexuality. Specimens contained largely spent gametes and were difficult to sex. From a sample of 25 individuals ranging in length from 10 to 30 mm, 12% had totally spent gonads, 12% appeared to have only female gametes and 76% were hermaphrodites.

TABLE 5. Sexuality of Brazos River *Corbicula fluminea*.

DATE		Length Size Class (mm)																				TOTAL
		6	8	9	10	12	13	14	15	16	18	20	21	22	23	24	25	28	29	30	33	
Sep. 1981	I	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
	F	4	—	—	—	4	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	9
	H	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—	5	—	—	8
Oct. 1981	F	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	2	—	4
	H	—	—	—	—	—	—	5	—	—	—	—	—	—	—	3	—	—	—	3	—	11
Nov. 1981	I	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2
	F	—	—	3	—	—	—	5	—	—	—	—	—	2	—	—	—	—	—	—	—	10
	H	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	5	—	—	—	8
Dec. 1981	I	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
	F	—	—	4	—	—	—	2	—	—	—	—	—	—	3	—	—	—	—	2	—	11
	H	—	—	—	—	—	—	3	—	—	—	—	—	—	2	—	—	—	—	3	—	8
Jan. 1982	F	—	1	—	—	—	—	2	—	—	—	—	—	—	—	2	—	—	—	1	—	6
	H	—	4	—	—	—	—	3	—	—	—	—	—	—	—	3	—	—	—	4	—	14
Feb. 1982	I	—	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
	F	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1
	H	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	2
Mar. 1982	F	—	—	—	—	—	—	—	4	—	—	2	—	—	—	—	—	—	—	—	3	9
	H	—	—	—	—	—	—	—	1	—	—	3	—	—	—	—	2	—	—	—	1	7
Apr. 1982	F	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	3	—	—	—	—	4
	H	—	—	—	5	—	—	—	—	2	—	—	5	—	—	—	2	—	—	—	—	14
May 1982	I	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
	F	—	—	3	—	—	—	—	—	—	1	—	—	—	—	3	2	—	—	1	—	10
	H	—	—	1	—	—	5	—	—	—	4	—	—	—	—	2	3	—	—	4	—	19
Size class totals:		7	10	15	5	4	5	20	5	3	5	5	5	12	5	15	12	5	5	20	4	167

	N	%
I = Immature.....	12	——
F = Female.....	64	41.3
H = Hermaphrodite..	91	58.7

Pinto Creek

The pattern of sexuality for Form A *Corbicula* at Pinto Creek is different from that observed for Brazos River specimens (Table 6 and Fig. 16B). In a sample of 162 sexually mature specimens ranging in length from 7 to 18 mm, 88.9% were females and 11.1% hermaphrodites. Although the proportion of females to hermaphrodites varies slightly with size, the number of females exceeds the number of hermaphrodites at all size classes (Fig. 16B). The pattern of sexuality for Form B *Corbicula*, however, is very different from that of Form A (Table 6 and Fig. 16C). In a sample of 138 sexually mature specimens ranging in length from 7 to 16 mm, 64.9% were hermaphrodites and 35.1% were females. As with the Brazos River population, the number of hermaphrodites exceeds the number of females at most size classes (Fig. 16A, C). The combined Pinto Creek population (Form A + Form B)

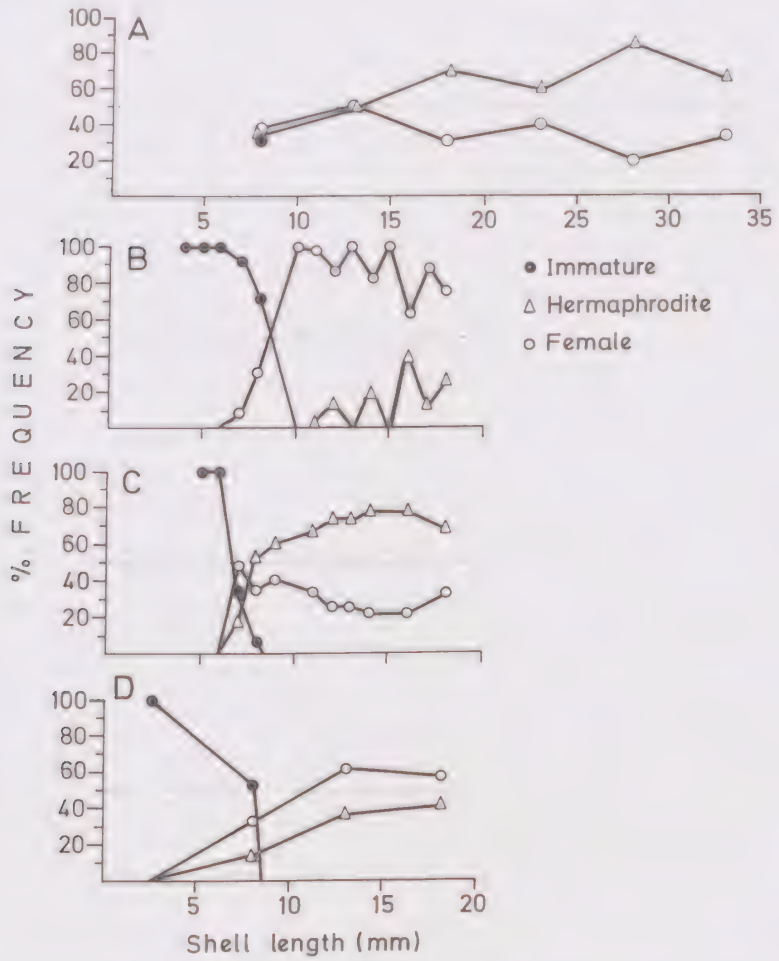

FIG. 16. Sexuality of *Corbicula fluminea* from the Brazos River, Hood-Sommerville Co., Texas (A), and locality N (Fig. 5), Pinto Creek, Kinney Co., Texas (B, C and D). Sexuality was determined by examination of histological sections of whole animals stained with Ehrlich's haematoxylin or Masson's trichrome. Sexuality is shown by percent frequency plots of sexually immature (closed circles), exclusively ovigerous gametes (females indicated by open circles) or a mixture of ovigerous and spermatogenic gametes (hermaphrodites indicated by open triangles). Abscissas represent length size classes in mm; ordinates represent the number of animals expressing a particular sexuality at a given length class expressed as a percentage of the total sample at that length class. **A**, Brazos River Form A morphotypes, N = 167. **B**, Pinto Creek Form A morphotypes, N = 228. **C**, Pinto Creek Form B morphotypes, N = 164. **D**, Pinto Creek, combined Form A and Form B morphotypes, N = 392.

fails to resemble the sexuality observed in the Brazos River, due largely to the overwhelming dominance of Form A females (Fig. 16D).

Despite the different expressions of sexuality in Form A and Form B Pinto Creek *Corbicula*, growth and reproductive periodicity of both forms are very similar to those observed for *C. fluminea* from many localities (Fig. 13). As with the Brazos populations, pediveligers are brooded and released during spring and fall, with distinctive periods of spring and autumn growth and winter and midsummer quiescence.

Phoenix Country Club, Arizona

Corbicula fluminea was sampled to determine patterns of sexuality from several localities in and around the Phoenix Country Club. The results varied considerably (Table 7). All 10 Form A individuals (shell length, 12-16 mm) sampled from the canal at the junction of 12th and Osborne streets (Fig. 7A) were female, but 19 Form B individuals (shell length, 8-14 mm) from the same site comprised 16% immature, 16% females and 68% hermaphrodites. Excluding the immature specimens, the sample

TABLE 6. Sexuality of *Corbicula fluminea* at Pinto Creek, Kinney Co., Texas (locality N, Fig. 5).

TOTAL	Form A Length Size Class (mm)															SEX	DATE	SEX	Form B Length Size Class (mm)									TOTAL
	4	5	6	7	8	10	11	12	13	14	15	16	17	18					5	6	7	8	11	12	13	14	16	
1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	I	Sep. 1981	I	–	–	–	–	–	–	–	–	–	–	0
4	–	–	–	–	–	–	–	4	–	–	–	–	–	–	F		F	–	–	–	1	–	–	1	–	–	–	1
0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	H		H	–	–	–	–	–	4	–	–	–	4	4
3	–	–	–	–	–	–	3	–	–	–	–	–	–	–	F	Oct. 1981	F	–	–	–	–	2	–	–	–	–	–	2
0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	H		H	–	–	–	–	3	–	–	–	–	–	3
3	–	–	–	–	–	–	3	–	–	–	–	–	–	–	F	Nov. 1981	F	–	–	–	–	–	–	–	–	–	–	0
0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	H		H	–	–	–	–	5	–	–	–	–	–	5
3	–	–	–	3	–	–	–	–	–	–	–	–	–	–	I	Dec. 1981	I	–	–	–	2	2	–	–	–	–	–	4
7	–	–	–	2	–	–	5	–	–	–	–	–	–	–	F		F	–	–	–	3	3	–	–	–	–	–	6
4	–	–	–	4	–	–	–	–	–	–	–	–	–	–	I	Jan. 1982	I	–	–	–	–	–	–	–	–	–	–	0
6	–	–	–	1	–	–	–	–	5	–	–	–	–	–	F		F	–	–	2	–	–	–	2	–	–	–	4
0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	H		H	–	–	1	–	–	–	3	–	–	–	4
2	–	–	–	2	–	–	–	–	–	–	–	–	–	–	I	Feb. 1982	I	–	–	–	–	–	–	–	–	–	–	0
7	–	–	–	3	–	–	–	–	4	–	–	–	–	–	F		F	–	–	1	–	–	–	2	–	–	–	3
0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	H		H	–	–	4	–	–	–	3	–	–	–	7
3	–	–	–	3	–	–	–	–	–	–	–	–	–	–	I	Mar. 1982	I	–	–	–	–	–	–	–	–	–	–	0
10	–	–	–	2	–	–	4	–	–	4	–	–	–	–	F		F	–	–	1	–	–	–	1	2	–	–	4
2	–	–	–	–	–	–	1	–	–	1	–	–	–	–	H		H	–	–	1	–	–	–	4	3	–	–	8
5	–	–	–	2	3	–	–	–	–	–	–	–	–	–	I	Apr. 1982	I	–	–	–	–	–	–	–	–	–	–	0
11	–	–	–	–	–	–	–	–	–	6	–	–	3	2	F		F	–	–	–	–	2	–	–	–	–	–	2
0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	H		H	–	–	–	–	3	–	–	–	–	–	3
7	–	–	–	7	–	–	–	–	–	–	–	–	–	–	I	May 1982	I	–	–	–	1	–	–	–	–	–	–	1
7	–	–	–	–	–	–	–	–	5	–	–	2	–	–	F		F	–	–	–	1	–	–	–	–	–	–	1
3	–	–	–	–	–	–	–	–	–	–	–	3	–	–	H		H	–	–	–	2	–	–	–	–	–	–	2
5	–	5	–	–	–	–	–	–	–	–	–	–	–	–	I	Jun. 1982	I	1	–	–	3	–	–	–	–	–	–	4
13	–	–	–	–	–	–	5	–	–	–	5	–	3	–	F		F	–	–	–	–	–	–	–	–	–	–	0
1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	H		H	–	–	–	–	–	–	5	–	–	–	5
4	4	–	–	–	–	–	–	–	–	–	–	–	–	–	I	Jul. 1982	I	5	–	–	–	–	–	–	–	–	–	5
9	–	–	–	–	–	–	5	–	–	–	–	4	–	–	F		F	–	–	–	–	1	–	–	1	–	–	2
1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	H		H	–	–	–	–	4	–	–	4	–	–	8
5	–	–	–	5	–	–	–	–	–	–	–	–	–	–	I	Aug. 1982	I	–	–	3	–	–	–	–	–	–	–	3
19	–	–	–	–	–	5	5	–	–	–	5	–	4	–	F		F	–	–	2	–	–	–	3	–	2	–	7
1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	H		H	–	–	–	–	–	–	2	–	3	–	5
5	–	–	5	–	–	–	–	–	–	–	–	–	–	–	I	Sep. 1982	I	–	–	–	–	–	–	–	–	–	–	0
9	–	–	–	–	–	–	5	–	–	–	–	3	–	1	F		F	–	–	–	4	–	–	–	1	2	–	7
1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	H		H	–	–	–	1	–	–	–	3	3	–	7
5	–	5	–	–	–	–	–	–	–	–	–	–	–	–	I	Nov. 1982	I	–	5	–	–	–	–	–	–	–	–	5
10	–	–	–	–	–	–	–	–	5	–	–	5	–	–	F		F	–	–	–	–	–	–	–	–	–	–	0
0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	H		H	–	–	–	–	–	–	–	4	–	–	4
5	–	–	5	–	–	–	–	–	–	–	–	–	–	–	I	Dec. 1982	I	4	–	–	–	–	–	–	–	–	–	4
8	–	–	–	–	–	3	–	–	–	3	–	–	–	–	F		F	–	–	–	–	–	1	–	–	1	–	2
7	–	–	–	–	–	–	–	–	–	2	–	5	–	–	H		H	–	–	–	–	–	3	–	–	4	–	7
4	–	–	–	–	4	–	–	–	–	–	–	–	–	–	I	Jan. 1983	I	–	–	–	–	–	–	–	–	–	–	0
11	–	–	–	–	1	–	–	5	–	–	–	–	5	–	F		F	–	–	–	3	–	–	–	1	–	1	5
0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	H		H	–	–	2	–	–	–	4	–	4	10
4	–	–	–	4	–	–	–	–	–	–	–	–	–	–	I	Mar. 1983	I	–	–	4	–	–	–	–	–	–	–	4
3	–	–	–	–	–	–	–	3	–	–	–	–	–	–	F		F	–	–	1	–	–	–	–	–	–	–	1
2	–	–	–	–	–	–	–	2	–	–	–	–	–	–	H		H	–	–	–	–	–	–	5	–	–	–	5
228	4	15	10	23	23	10	40	14	19	16	10	23	17	4	<N per size class>			10	5	25	22	20	9	35	18	20	164	

	FORM A		FORM B	
	N	%	N	%
I = Immature.....	66	----	30	----
F = Female.....	144	82.9	47	35.1
H = Hermaphrodite..	18	11.1	87	64.9

TABLE 7. Sexuality of *Corbicula fluminea* from localities in the vicinity of the Phoenix Country Club, Phoenix, Maricopa Co., Arizona.

LOCALITY (Fig. 7)	FORM	Length Size Class (mm)																								% FEMALE	% HERMAPHRODITE
		8			9 12		13		14		16		18	20	22	24		26		28		30		32	34		
		I	F	H	F	F	F	H	F	H	F	H	H	H	H	F	H	F	H	F	H	F	H	F	F		
A	A	-	-	-	-	6	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	100	0
	B	3	3	3	-	-	1	6	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19	81
C	A	-	-	-	8	-	8	-	-	-	7	3	-	-	-	-	-	-	-	-	-	-	-	-	-	88.5	11.5
	B	-	-	-	-	-	-	-	-	-	-	-	1	1	2	1	-	-	-	-	-	-	-	-	-	20	80
D	A	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	2	-	1	1	-	-	-	-	50	50
	B	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1	2	-	1	1	2	3	72	18
Totals:		3	3	3	8	6	9	6	1	3	11	3	1	2	2	1	1	3	1	3	1	1	1	2	3		

I = IMMATURE F = FEMALE H = HERMAPHRODITE

comprised 19% females and 81% hermaphrodites. Of 26 Form A individuals (shell length, 9-16 mm) sampled from the Osborne Street canal (Fig. 7B), 88.5% were female and 11.5% were hermaphrodite. In the pond beside Fairway 15 (Fig. 7D), 11 Form A individuals (shell length, 14-34 mm) comprised 18% hermaphrodites and 72% females.

Thus, the sexuality observed for Forms A and B morphs from these Phoenix Country Club localities conform to the general pattern established for these two forms at Montezuma Well and Pinto Creek. Form A comprises a high incidence of females (> 80%), whereas Form B is characterized by a high incidence of hermaphrodites (> 80%).

In the Country Club pond near Fairway 12 (Fig. 7C), however, five individuals considered to be Form A (shell length, 18-24 mm) were 80% hermaphrodite and 20% female, whereas six Form B individuals (shell length, 22-28 mm) were 50% hermaphrodite and 50% female. One would have expected a greater incidence of females, particularly with respect to Form A. All of these specimens were large individuals and it has been shown among Pinto Creek specimens that the incidence of hermaphroditism in Form A increases with size. The particular problems of the ponds in the club grounds will, however, be discussed.

DISCUSSION

North American Forms A and B *Corbicula* are either separate species or individuals of distinct phenotypes belonging to a single polymorphic species. Morphometric and (to date) electrophoretic evidence suggest a two-species model (Hillis & Patton, 1982; McLeod, 1986), whereas ecological, distributional, reproductive, growth and limited physiological data from native Asian and North American populations suggest there is a single, highly adaptable polymorphic species (this paper). No single criterion (e.g., morphology, allozyme genetics, reproductive state, habitat, etc.) can adequately resolve the problem. Furthermore, there are additional factors, including the nature of molluscan polymorphism, heterozygote deficiency and selection pressure, which must be considered.

Molluscan polymorphism may be phenotypic, genotypic, or both. Allozyme protein polymorphism may be extensive, even in the absence of phenotypic polymorphism (Wilkins & Mathers, 1973; Torigoe, 1978). However, the best studied forms of molluscan polymorphism are phenotypic, related to shell shape and shell or body color.

Form variation and color polymorphism are well known among molluscs occupying intertidal, freshwater and terrestrial habitats (Simpson, 1976; Hoagland, 1977; Gill, 1978; Dando et al., 1981; Beaumont, 1982). Color polymorphism is particularly prevalent among gastropods, and several studies have demonstrated strong correlations between environment and expressions of color morphotypes. Shell color in the polymorphic land snail *Xeropicta vestalis* is positively related to the extent of perennial vegetation (Heller & Volokita, 1981). The land snail *Cepaea nemoralis* is highly color polymorphic, with natural populations usually comprising two or more morphotypes. The distribution of *C. nemoralis* color morphs is highly correlated with certain environmental factors, suggesting a strong role for selection (Cain & Sheppard, 1950, 1952, 1954; Sheppard, 1951, 1952). Tilling (1983) has shown that color polymorphism in *C. nemoralis* plays an important role in determining behavioral responses of these snails to their environment and that thermal relationships are potentially important causative

factors in natural color polymorphism. Shell and tissue color polymorphism also have been described for *Crepidula* spp. (Franz & Hendler, 1970; Hoagland, 1977), *Thais* (Spight, 1976), *Cepaea* sp. (Cain & Sheppard, 1950) and *Bradybaena* sp. (Komai & Eonura, 1955). Franz & Hendler (1970) and Spight (1976) discussed distinct environmental influences upon the distribution of color morphs.

Shell shape or form has been shown to vary according to environmental conditions (notably with regard to the degree of exposure) in many intertidal gastropods, including limpets (Moore, 1934; Rao & Ganapati, 1971), littorines (Heller, 1976; Van Marion, 1981), *Neritina* (Murty & Rao, 1978) and *Nucella lapillus* (Kitching, 1977; Crothers, 1983). Littorine snails perhaps illustrate best the taxonomic problems that polymorphism imposes. Most modern taxonomists agree on the split of the former *Littorina saxatilis* species complex into four distinct species (Hannaford-Ellis, 1979). Many populations of these "species", however, are highly polymorphic (Pettitt, 1973; Atkinson & Warwick, 1983) and much debate revolves around the precise status of *L. arcana*. Some authors, e.g., Ward & Warwick (1983), Atkinson & Warwick (1983) and Ward & Janson (1985), regard *L. saxatilis* and *L. arcana* as closely related but separate species. Because they can only be unambiguously separated with respect to the structure of the female reproductive tract, several authors, e.g., Caugant & Bergerard (1981) and Hughes & Roberts (1981), argue that *L. arcana* is no more than a reproductive morph of *L. saxatilis*. Similar arguments are developing with regard to the *L. scabra* species complex in Indo-Pacific mangroves (Hughes & Jones, 1985). The significance of this debate will become more apparent in the succeeding discussion on *Corbicula fluminea*.

Form variation and color polymorphism are known also among the Bivalvia. We have long known that the shape and thickness of certain unionid, mytilid and oyster shells vary according to specific environmental conditions. Much of the difficulty associated with species recognition in intertidal mussels and oysters has been due to this kind of polymorphism. For example, the length/width ratio of *Crassostrea virginica* is significantly greater among oysters growing upon a soft substrate than among oysters within the same area living upon a hard bottom (Orton, 1936; Gunter, 1938). *Geukensia demissa* size and growth rate in Chesapeake Bay vary according to changes in the physical environment (Bertness, 1980). *Corbicula fluminea* shell shape varies according to flow conditions (Britton & Morton, 1979), and sphaeriid shell shape is variable, depending upon the specific environment (Mackey, 1984). For the corbiculid *Polymesoda caroliniana* at least three shell morphs have been recognized. A broad morph from Louisiana has been shown to be statistically different from the others, these forming a continuum with overlap between populations (Hackney, 1985). This author concluded that such variations in shell morphology likely were due to genetic and/or environmentally induced mechanisms.

Until recently, color polymorphism has been little studied in the Bivalvia. During the last decade, however, research upon certain intertidal Mytilacea (Koehn et al., 1976; Levinton & Koehn, 1976; Waldron et al., 1976; Ahmad et al., 1977; Innes & Haley, 1977; Kartavtsev, 1978; Newkirk, 1980; Colgan, 1981) and Ostreacea (Fujio, 1979; Zouros et al., 1980; Singh & Zouros, 1981) suggests that color polymorphism may be more widespread in this class than hitherto believed. *Mytilus edulis* is especially well known for color polymorphism (Coe & Fox, 1942; Fox & Coe, 1943; Stasek, 1963; Seed, 1968; Waldron et al., 1976; Innes & Haley, 1977; Newkirk, 1980). Innis & Haley (1977) presented data which suggest shell color in *M. edulis* is determined by a single locus-two allele model: individuals homozygous for a recessive allele are blue. Newkirk (1980) confirmed shell color to be controlled by "a relatively simple genetic mechanism . . . for the most part consistent with the single locus model." However, he also recognized the possibility of one or more dominant alleles at the locus having a lesser influence upon shell color. In either case, only a few alleles representing perhaps no more than a single locus are responsible for a degree of color variation in *M. edulis* comparable to that observed in *Corbicula fluminea*.

Only within recent years have studies emerged which assess causative factors or consequences of molluscan polymorphism. Several authors have stressed the importance of small founder populations in the establishment and maintenance of polymorphism (Cook & Pettitt, 1979; Gartner-Kepkay et al., 1980; Badino & Celebrano, 1981). Hoagland (1977) has emphasized the point that organisms which must cope with changing environments tend to express a degree of phenotypic plasticity and polymorphism not seen in organisms restricted to homogeneous environments. Foltz et al. (1984) recognized considerable genotypic polymorphism which is also expressed in environment-specific phenotypes in the parthenogenetic snail *Potamopyrgus jenkinsi*. In this case, polymorphism apparently is enhanced by the absence of genetic exchange between mating pairs (i.e., within clonal lines); a similar, although not parthenogenetic, condition is likely applicable to *Corbicula fluminea*.

It should come as no surprise, therefore, that *Corbicula fluminea*, generally agreed to have become

established in North America by small founding populations and widely recognized as capable of surviving in several different environmental situations, is polymorphic with respect to form and color. This polymorphism occurs in both North American and native Asian populations. At least two color morphs are known to occur among *C. fluminea* living in Hong Kong irrigation furrows (Morton, unpubl. data). North American specimens which lack color polymorphism nevertheless may display shell form plasticity, as has been demonstrated by Britton & Morton (1979, figs. 7, 10, pp. 265, 271). The question not yet satisfactorily answered concerning *Corbicula* is the genetic basis for the polymorphism and whether or not it is environmentally mediated.

During the last two decades, procedures to discriminate subtle differences among enzymatic proteins have emerged as a biochemical tool to detect genotypic polymorphism. Using data derived from protein electrophoresis, difficult species groups have sometimes been discriminated by biochemical or genotypic differences. Supraspecific taxa are best served by the technique (e.g., Hornbach et al., 1980; Davis & Fuller, 1981; Hoagland & Turner, 1981), but isozyme or allozyme differences have been employed for discrimination at the species level as well (Coduri & Rand, 1972; Kodolova & Logvinenko, 1974; Park et al., 1974; Buroker et al., 1979a,b; Skibinski et al., 1980; Badino & Celebrano, 1981; Hillis & Patton, 1982). Such techniques might arguably be more objective than traditional phenetic taxonomic methods for decision making at the species level. The degree of allozyme polymorphism and variability have proven to be considerably greater and more complex than originally expected. Homozygote excess (heterozygote deficiency), environmental influence of gene frequency, Wahlund effects, differential reproductive strategies within a species, and diet are only some factors which have been reported to influence allozyme frequency and bring into question the validity of protein biochemistry for species differentiation.

The bivalve genetics literature is replete with examples of homozygote excess, and a number of factors have been suggested which may account for it. Genetic drift and the Wahlund effect associated with small founding populations commonly have been cited (Koehn et al., 1976; Kartavtsev, 1978; Fujio, 1979; Beaumont et al., 1980; Gartner-Kepkay et al., 1980; Kat, 1982). Null alleles which can influence electrophoretic scoring sometimes have been implicated (Milkman & Beatty, 1970). Colgan (1981) argued against several of these factors in favor of natural selection. Homozygote excess has been associated with variations in color, size, the differential expression of sexuality within populations and selection pressure, and occurs most frequently among populations transcending several microhabitat boundaries.

Several studies have shown that homozygote excess is more prevalent in smaller individuals (*Modiolus*: Koehn et al., 1973; *Mytilus*: Tracey et al., 1975; oysters: Singh & Zouros, 1978, 1981; Zouros et al., 1980). When homozygote excess is more prevalent in larger size classes, as in the scallops *Chlamys opercularis* (Beaumont, 1982) and *Pecten maximus* (Wilkins, 1978), self-fertilization cannot be an important component of reproduction. These and other authors (e.g., Powell, 1971) considered that homozygotes are best adapted to specific environmental conditions with heterozygosity most beneficial in variable environmental situations.

Homozygote excess frequently has been attributed to environmental selection pressures. Beaumont (1982) maintained that homozygote excess in larger *Chlamys opercularis* is due to selection acting at larval and juvenile stages. Koehn & Mitton (1972) attributed heterozygote deficiency in *Mytilus edulis* to selection. Higher zoned *M. edulis* living under more rigorous environmental conditions than lower zoned individuals also had a greater frequency of homozygotes, again suggesting increased selection (Koehn et al., 1973). Lassen & Turano (1978) found marked heterozygote deficiency within the environmental cline between estuarine and open ocean populations of *M. edulis*, reinforcing the concept of homozygote excess in difficult environmental situations. Gosling & Wilkins (1981) noted different allele frequencies between exposed and sheltered populations of *M. edulis* and *M. galloprovincialis* on Irish coasts. Similarly, Theisen (1978) reported significant differences in allozyme frequencies between *M. edulis* populations from Baltic and North Sea localities, and observed strong differential mortality among individuals transplanted from one locality to the other. Thus, allozyme frequency can be significantly influenced by environmental selection. Koehn et al. (1980) discussed the mechanisms by which salinity variations influence allele frequencies of aminopeptidase-1 in *M. edulis*.

Selection can act most effectively if there is concurrent subdivisioning and partitioning of the reproductive population (Tracey et al., 1975). Differential sexuality is unusual but not unknown among the Bivalvia, especially for species occupying a range of habitats. Smith (1979) has shown that *Margaritifera falcata* can be dioecious or hermaphroditic. Similarly, *Anodonta cygnea* may be dioecious (gonochoristic) in running waters whereas hermaphroditic in ponds (Wiesensee, 1916; Bloomer, 1939). Morton (1983) similarly reported different sexual strategies for *Corbicula fluminea* in lentic and lotic

waters. With different expressions of sexuality among populations, the chance of extreme homozygote excess is enhanced, although Colgan (1981) considered homozygote excess in *Brachidontes* largely attributable to selection pressures.

Considerable enzyme polymorphism may facilitate the colonization of new habitats (Badino & Celebrano, 1978); conversely, a changing environment may act to induce the expression of specific, previously latent allozymes. The chemical medium (Gill, 1978), temperature (Koehn, 1971), degree of exposure and salinity (Koehn et al., 1980) are some environmental conditions influencing the frequency of expression of certain enzymes. Varying frequencies of allozyme polymorphs along latitudinal gradients may reflect temperature influences upon these enzymes (Koehn, 1971; Koehn et al., 1980).

Gene-linked changes necessarily require several generations for expression and frequently are associated with the development of diversity within populations originating from a small number of founders. The eastern and western *Corbicula* populations studied by McLeod (1986) are excellent examples of this kind of environmentally engendered diversity. The source of variation within these populations may be masked alleles or mutations, but the gradualness of their expression is clear. More accelerated changes in allozyme frequencies are usually correlated with selective pressures in specific environmental situations where homozygote excess is favored (Koehn, 1971).

The sexuality of populations can influence the phenotypic and genotypic composition of a population. Tracey et al. (1975), for example, concluded that homozygote excess in *Mytilus californicus* is in part the result of subdivisions of the reproductive population. Many workers have suggested a relationship between self-fertilization and heterozygote deficiency. Selander & Kaufman (1973) implicated self-fertilization as a causative factor for heterozygote deficiency in land snails, as did Thomas (1959) and Hornbach et al. (1980) for *Sphaerium*. The latter authors further pointed out that genetic variability among four species of *Sphaerium* is extremely low compared to that of other invertebrates (mean heterozygosity per population, 0.38%), and this can be attributed to self-fertilization or selection against heterozygotes. The situation with *Corbicula fluminea*, a closely related bivalve, is similar but even more extreme; that is, the reported homozygote excess (Hillis & Patton, 1982; McLeod, 1986) is entirely explainable by the environmental induction of a single species into morphological types which pursue different reproductive strategies, characterized by different degrees of hermaphroditism.

Selander & Hudson (1976) attributed low genetic diversity in introduced North American populations of *Rumina decollata* to a small founding event and maintenance by inbreeding with little outcrossing. They also predicted this condition would be found to be of adaptive value for a variety of sessile and semi-sessile organisms. Smith et al. (1979), McLeod & Sailstad (1981) and McLeod (1986) have suggested self-fertilization as a possible mechanism by which North American *Corbicula* populations have retained relatively low genetic diversity. Fujio et al. (1979) attributed homozygote excess of isocitrate hydrogenase to be the result of inbreeding populations. In contrast, Gartner-Kepkay et al. (1980) and Colgan (1981) minimized the role of inbreeding and self-fertilization as a mechanism favoring homozygote excess and instead strongly favored environmental selection as a primary causative factor.

Some polymorphic enzyme systems are inducible. For example, Gill (1978) has shown that significant inducible variation occurs in isozyme patterns of acid and alkaline phosphatase, and alpha-glucophosphate dehydrogenase in *Cepaea nemoralis* during feeding. Different electrophoretic patterns are obtained for these enzymes depending upon the proximity of a feeding event to specimen collection and examination. Similar diet-induced alterations in allozyme frequency have been shown to occur in *Drosophila* (Schwartz & Sofer, 1976). Arctic and northern temperate fish produce peptide and glycopeptide "antifreezes" in cold seasons, and cease synthesis of these substances in warm seasons (Gordon et al., 1961; Duman & DeVries, 1974; Raymond & DeVries, 1977).

Two mechanisms have been suggested to account for environmentally induced polymorphic enzymes. Organisms may possess "multiple variant" genes in which different allozymatic proteins are expressed according to different environmental conditions (Hochachka & Somero, 1973, pp. 245-246). The organism may maintain switching mechanisms to "turn off" inefficient isozymes when unneeded, as occurs in rainbow trout brain acetylcholinesterase. Another, less common mechanism involves "eurytolerant proteins", which adapt directly to environmental changes without the necessity for switching mechanisms. Gill (1978) suggested that one or both forms of isoenzymatic adaptation may be operative in *Cepaea nemoralis* and other molluscs demonstrating differential electrophoretic patterns brought about by environmental influences. Although Gill's work addresses short-term changes, there is no reason to exclude long-term isozyme induction brought about by exposure to specific environmental conditions. In fact, the extreme homozygote excess observed in certain isozymes of North American *Corbicula* populations may be the result of this kind of environmental induction operating

upon juvenile or developmental stages.

With all this in mind, consider now the possibility of two *Corbicula* species in North America. The initial reports of light and dark morphotypes of North American *Corbicula* (Fontanier, 1982; Hillis & Patton, 1982) indicated sympatric distribution of the morphs with possible habitat partitioning. Initially, our work at Pinto Creek locality N seemed to suggest a sympatric distribution but with no habitat partitioning. Additional work has shown, however, that the apparent sympatry at locality N is but an artifact of a more complex situation.

Despite Hillis & Patton's evidence for distinctly different morphologies between the two sympatric morphotypes, there is, in fact, considerable overlap between them. Color and shell form polymorphism in North American (and Hong Kong) populations of *Corbicula* is well within the range of variability expressed by other molluscs. Our additional observations at Pinto Creek and in Arizona streams also suggest that this variability may be strongly influenced by environmental conditions. Form A *Corbicula* tolerate a wide variety of aquatic environments, but tend to disappear under the specific set of conditions which favor Form B. The latter are mostly restricted to streams rich in calcium, and experiencing high pH, high summer temperatures, and chemical precipitation of travertine. Similar (but not identical) darkly pigmented *Corbicula* occur in other localities where some, but not all, of the above conditions are present (e.g., the Hong Kong dark forms, and the lightly purple shells from several southeastern U.S. localities). Thus, the existence of phenotypic intermediates between Form A and B extremes in both sympatrically and environmentally isolated populations make it very difficult to recognize a two-species model for North American *Corbicula* by morphological criteria.

There is reasonably strong distributional evidence that the Form B morphology is environmentally induced. Pinto Creek locality N is not the primary habitat for Form B specimens, and we suspect the same is true with respect to the San Gabriel locality from which Hillis and Patton obtained their specimens. Pinto Creek locality N is more accurately an ecotopic zone between the typical Form B habitat and the quite different Rio Grande, occupied exclusively by Form A. Both forms attain smaller adult size at locality N than at their respective sites of monomorphic occurrence. This could be the result of competition, but we found no evidence for it. More likely it indicates a less than optimal environment for both morphotypes. The density of either or both morphs at locality N was much lower than at localities C, I, the Brazos River or Montezuma Well irrigation canal, where only monomorphic populations are found. It is perhaps significant that Ramos (1985) has concluded for *Cepaea nemoralis* in Spain that peripheral variations in the environment are important in determining not only the occurrence of the species but also its genetic structure.

At least some of the Form B population at locality N were likely transported there from upstream populations, especially during the heavy flooding which occurred in May, October and November 1982 (Fig. 14). The presence of Form A at this locality is somewhat more difficult to explain; however, Golightly (1982) has demonstrated the ability of *Corbicula* to migrate upstream, which can account for colonization from the Rio Grande. Both forms are capable of producing surviving offspring at locality N, indicating environmental conditions here are not outside the limits of tolerance for either.

The presence of Form A at Pinto Creek localities B and C and their virtual absence from localities H to M suggests an environmental barrier excluding their presence at the latter sites. This is reinforced by the absence of Form A at the Montezuma Well site. Conversely, the striking disappearance of Form B in the water supply canal at the Phoenix Country Club supports the concept of an environmental barrier for this morph as well. The low frequency occurrence of Form B in downstream golf course ponds suggests a few specimens are washed past the zone of inhibition. They apparently are able to survive in the ponds as mature adults, but there is evidence (the absence of juveniles or young adults below a length of 15 mm) which suggests that neither morph can sustain a viable self-perpetuating population in the ponds.

The remaining evidence for a two-species model is biochemical. Information is now available on the allozyme variability of 22 North American Form A *Corbicula* populations (Smith et al., 1979; McLeod & Sailstad, 1981; Hillis & Patton, 1982; McLeod, 1986). There is remarkedly little genetic variability within these populations. The mean percentage of polymorphic loci for all populations is 4.41, with a range of 0-19% for any specific population. Only four populations have a greater than 10% polymorphism. The number of individuals heterozygous at a locus (averaged over all loci) is extremely low. Only five Form A populations displayed heterozygosity, ranging between 0.13% (Charlotte, North Carolina, U.S.A.) to 0.49% (Catawba River, North Carolina). Pinto Creek Form A *Corbicula* displayed no heterozygosity for any locus. This pattern of low polymorphism and little or no heterozygosity strongly indicates the organism to be a facultative self-fertilizing species (Selander &

Hudson, 1976; McLeod et al., 1981; McLeod, 1986). Under these circumstances, it seems more probable that a series of monomorphic races has become established as new populations are founded. In all local populations, cross fertilization is possible but typically infrequent. There is additional morphological evidence that Form A *Corbicula* are capable of self-fertilization (Britton & Morton, 1979; Kraemer, 1979).

Considerably less data are available for allozyme variation in Form B *Corbicula*. No more than 165 specimens from three localities have been examined by electrophoretic techniques: 50 specimens from the San Gabriel River, Texas (Hillis & Patton, 1982); approximately 25 specimens from Pinto Creek (Smith, Savannah River Ecology Laboratory, unpub. data); and no more than 90 specimens from Pinto Creek or Montezuma Well irrigation canal (McLeod, 1986). Neither Hillis & Patton nor Smith detected polymorphism or heterozygosity in their samples. McLeod reported polymorphism from Pinto Creek and Montezuma Well canal specimens and heterozygosity among Pinto Creek Form B *Corbicula*. Five of 11 enzymes examined from specimens collected at Pinto Creek locality N were found to be polymorphic. At least one of each of the polymorphic alleles also occurred in Pinto Creek locality N Form A *Corbicula*. Polymorphism frequency in this population was higher than that observed in any Form A population (22.72%). Only one enzyme, malic enzyme (ME) occurred as a mutually exclusive homozygote between Form A and B samples. Phosphoglucose isomerase 1 (PGI-1) was found to occur in Pinto Creek and Montezuma Well canal Form B specimens, but not in any Form A specimens tested.

In contrast to the relatively high polymorphism in Pinto Creek Form B *Corbicula*, the only enzyme displaying polymorphism in Form B specimens from the Montezuma Well irrigation canal was glutamate oxaloacetate transaminase 1 (GOT-1). One of its alleles also was found in both Form A and B Pinto Creek specimens.

If, as we have suggested: (1) *Corbicula* phenotype morphology is environmentally influenced, with the specific water conditions occurring in the Montezuma Well irrigation canal and Pinto Creek locality I being highly selective for the Form B morphotype; (2) Pinto Creek locality N represents a marginal or ecotypic environment slightly favoring Form A morphotypes but not strongly selecting against Form B; and (3) Form B occurs at Pinto Creek locality partly by downstream transport of "cloned" (reproduced by self-fertilization) individuals from a more highly selective environment and partially by self-fertilizing specimens at locality N under significantly less rigorous environmental pressure, then the high degree of polymorphism reported by McLeod (1986) can be explained. The picture is complicated, however, by the variable reproductive strategies employed by *Corbicula* and those portions of the life cycle most susceptible to environmental influences which can affect phenotypic polymorphism.

We hypothesize that developmental or juvenile life stages of *Corbicula* are most susceptible to environmental pressures which can generate polymorphism. Once induced, adult specimens seem to be fixed for the phenotypic changes. A subsequent generation, however, will be influenced by the immediate environment and presumably could revert to the prealtered phenotype which we believe to be the Form A morph. Three observations support this hypothesis.

First, it is very difficult to differentiate very young (2-6 mm) or large (> 25 mm) Form A or B morphs by shell characters. Even large specimens of Form B, of course, retain the completely purple shell interior, but shell shape and annuli tend to grade into that of comparably sized Form A morphs. Similarly, there are no readily detected shell features which serve to distinguish morphs in very young specimens. The shell interior of 2-6 mm specimens is uncolored, there is no significant difference in shell shape, and the pronounced differential annuli spacing that serves to distinguish 7-18 mm morphs is inconclusive at this stage. Thus, it seems the transformation from amorphic juvenile to Form A or B morphotype occurs at a shell length of about 4-8 mm, concurrent with the onset of sexual maturity. Once transformed, Form B morphs apparently retain the purple shell interior throughout their lives, despite the environment in which they are subsequently found.

Second, Form B *Corbicula* occur in Phoenix Country Club ponds in an environment clearly not typical for this morphotype. They occur, however, only as adults and only in very low frequencies. One can conjecture that if Form B is induced from Form A by environmental influences similar to those found in the Montezuma Well irrigation canal, induction of Phoenix specimens most likely occurs in a canal environment and not in the ponds. Once having occurred, however, it must be irreversible for any specific individual. Thus, Form B specimens occasionally pass the well water barrier and reside in the golf course ponds as Form B adults. This again supports the view that environment most strongly influences developmental or juvenile individuals.

Third, the slightly higher survivorship of Form A autumn spatfall might suggest some Form B juveniles develop into Form A adults. Throughout Pinto Creek, the autumn spatfall is released from environmental stress experienced by the parental generation during the previous spring or summer. Stress

likely takes several forms, but the most dramatic in this habitat involves the precipitation of calcium carbonate as travertine, and the consequential depletion of these ions in areas lacking a source for replenishment (e.g., locality N). Where groundwater sources provide local replenishment (and even possible excess), such as immediately downstream from Stricklin Spring, Form B thrives. In marginal environments, such as locality N, its numbers fluctuate, perhaps supported or periodically boosted by an influx of immigrants from upstream sources following floods. Despite the complicating factor of immigration, Form B frequencies still decline during the winter when flooding is not prevalent. The chemical environment at locality N is apparently suboptimal for Form B *Corbicula*. This morph experiences greater mortality here and never attains the larger sizes commonly seen only a few km upstream. However, the environment is sufficient to ensure survival and even reproduction, as Form B juveniles are being produced here, and serve to increase the frequency of the morph following the spring spatfall (immigration from upstream localities notwithstanding). Spring marks the return of conditions in which Form B apparently thrives. Under these circumstances, one must seriously consider the possibility that a portion of the Form B autumn spatfall at locality N develops into Form A adults the following spring, whereas the spring spatfall experience conditions conducive for development of Form B adults.

The Form B population at Pinto Creek locality N is almost certainly composed of elements derived from two different chemical environments. Some passed a juvenile stage upstream in an environment similar to that at localities I, J or K and were transported to locality N by flooding. The other portion of the population was derived from Form B specimens presently reproducing at locality N. Both groups are apparently employing self-fertilization as the primary (but not exclusive) method of reproduction. Little genetic variability should be expected from either element of the Form B population. Such is not the case.

The enzyme polymorphism found by McLeod (1986) in Form B at locality N is not likely to be the result of self-fertilization, for we have seen that this method of reproduction favors homozygosity. Despite a mixed Form B population, both sources (local and upstream) employ the same method of reproduction. Thus, the only variable remaining to account for a relatively high degree of genetic variability in Form B at locality N is the environment. In a non-marginal environment (Montezuma Well canal), there is very little enzyme polymorphism and virtually no phenotypic polymorphism. Unfortunately, the genetic variability of Pinto Creek locality I specimens remains to be tested, but according to the foregoing hypothesis, one would expect specimens from this locality to show limited enzyme polymorphism also.

We conclude that there is insufficient evidence to justify a two-species model for North American *Corbicula*. The preponderance of evidence supports the view that a single highly variable species, *C. fluminea*, is presently the only introduced freshwater corbiculid in North America. *Corbicula fluminea* is relatively variable throughout its natural and introduced ranges, with at least two distinctive morphotypes which differ by color and shell morphology.

The predominant form has a white-cream shell interior occasionally streaked with light purple antero- and posterodorsally. The sexuality of this form may be simultaneously hermaphroditic, seasonally hermaphroditic, hermaphroditic and female (each of these types are known in both Asia and North America), or gonochoristic with distinct males and females (to date only observed in Asia (Morton, 1983)). The sexual state observed at any specific locality may reflect seasonal production of male gametes (Heinsohn, 1958; Coldiron, 1975; Kraemer & Lott, 1977), environmental influences (Morton, 1983), or both. Coe (1941) recognized the expression of sexuality in some freshwater bivalves could be environmentally influenced: "the sex differentiating mechanism is so delicately balanced between the two sexual tendencies (hermaphroditism vs gonochorism) that relatively slight differences in environmental conditions may be potent in determining which of the two contrasted aspects of sexuality shall be realized." We have cited many examples of other molluscs in which phenotypic features other than sexuality also can be environmentally altered, and we suggest that similar kinds of polymorphism can occur in *Corbicula fluminea*.

The dark morph is a case in point. Our data suggest that it is derived from the predominant North American phenotype. Under appropriate environmental stimuli, purple blazes on juvenile shells expand to color the entire shell interior uniformly purple. In the United States, this color morph is usually restricted to flowing water traversing limestone bedrock in regions which experience high summer water temperatures and chemical precipitation of travertine. Dark morphs are rarely found in lentic waters, and their occasional presence in this habitat usually can be attributed to transport via lotic sourcewaters (e.g., as in the Phoenix Country Club ponds). The consistent habitat relationship with the dark morph and the presence of intermediate morphologies when some but not all of the described conditions are present suggests that the dark morph is derived and sustained by environmental factors. Sexually, the Form B is predominantly hermaphroditic with a low frequency of female gonochorism.

Self-fertilization is likely the most common method of reproduction, producing large numbers of offspring with relatively low genetic variability within the morphotype, but having certain allozymes markedly different from those of Form A as a result of environmental influences. Form B grows more slowly than Form A, possibly causing external sulcations on the shell to be more narrowly spaced, especially within the first 20 mm of shell length. The lifespan of the dark form is shorter in environments where light and dark morphs coexist, but, under optimal environmental conditions, dark morphs can become as large and presumably at least as old as the light morph (slower growth in Form B could argue for older ages for this morph in equal-length specimens of both morphotypes).

Abdel-Rehim (1984) has shown that the brown and yellow morphs of the land snail *Arianta arbustorum* have different metabolic rates resulting from different responses to microclimatic factors. As temperature and humidity also affect the nocturnal activity of the color morphs of this species (Abdel-Rehim, 1983), it would seem that growth rates too would be different – a situation which we believe has strong homologies with *Corbicula fluminea*.

Ramos (1985) has arrived at essentially similar conclusions with regard to two morphs of *Cepaea nemoralis* in Spain. Each occupies its own biotope but, in peripheral situations, environmental conditions are important not only in determining the distribution of the species, but exert a marked effect on the genetic structure of the populations.

The dark morph apparently has a selective advantage under specific environmental influences. The mechanism by which the environment induces these changes is unknown. Whether or not it is through the direct or indirect effects of natural selection or whether or not some other processes, including genetic assimilation, remains for future experimentation. These influences affect a variety of potentially polymorphic allozyme proteins, with phenotypic consequences most obvious in shell form and color. Environment may also produce somewhat different reproductive strategies among morphotypes, with Form A largely female most of the year ($> 80\%$) but with a small percentage of hermaphrodites always in the population. In contrast, hermaphrodites dominate the Form B population throughout the year. The propensity of *Corbicula fluminea* to develop different reproductive strategies in different environments may help reinforce phenotypic differences between morphotypes.

Corbicula fluminea seems most susceptible to environmental influences during juvenile or developmental stages, and once an individual is altered the changes are possibly irrevocable. We hypothesize that the shell and enzyme morphology of Form B morphotypes is influenced or induced by a specific set of environmental conditions.

ACKNOWLEDGEMENTS

This research was initiated during B. Morton's tenure as the Green Honors Chair Professor at Texas Christian University in the fall of 1981. He is grateful to Cecil and Ida Green, who provided the endowment for the Chair, and to Texas Christian University, which provided the opportunity and facilities for work in the United States. This paper is but one of several collaborative and interactive accomplishments made possible by the Chair appointment.

This work was supported primarily by research grants from the Texas Christian University Research Fund awarded to J. Britton. During the course of the project, several students and colleagues assisted in the field, including David Britton, Mark Britton, Sam Brush, Larry Champagne, Larry Cooke, Allison Craig, Lisa Fitzgerald, Jerry Landye, C.E. Murphy and John Schofield. We are appreciative of the permission provided by several landowners along Pinto Creek, Texas, which enabled us to enter their private land and observe critical areas which otherwise would have been inaccessible.

The study of Arizona populations would not have been possible without the aid of several organizations and individuals. We appreciate the assistance of the management of the Phoenix Country Club, and especially that of Leonard Marlow, Green Superintendent, who provided us access to the waterways of the Country Club grounds and considerable information on the history of *Corbicula* at this locality. We are equally indebted to the National Park Service, U.S. Department of Interior, for permission to study the *Corbicula* population in the irrigation canal at Montezuma Well National Monument. We are especially appreciative of the encouragement and information provided by Glen E. Henderson, Superintendent of Montezuma Castle and Tuzigoot National Monuments. Jerry Landye of the Arizona Game and Fish Department also was helpful in providing transportation and access to other *Corbicula* localities during one trip to Arizona.

Water chemistry analyses were performed by John Schofield at Texas Christian University. H.C. Leung (University of Hong Kong) prepared the histological sections for the reproductive study.

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Malacological Review, 1986, 19: 45-52

EMBRYONIC EXPRESSION OF SHELL DIMORPHISM IN *MARGARITES VORTICIFERA* (GASTROPODA: TROCHIDAE)

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ABSTRACT

Evidence was sought for shell dimorphism in embryos of *Margarites vorticifera*, a brooding archaeogastropod possessing adult shell sexual dimorphism. Data from stereo-pairs of scanning electron micrographs were subjected to multivariate statistical analysis. Two structurally distinct shell types are present among brooded embryos, as determined both by cluster analysis and discriminant function analysis. Embryonic shell dimorphism is based on the position of the generating curve relative to coil axis. Statistical analyses were better able to detect embryonic dimorphism than was visual inspection of micrographs. This is the first report of shell sexual dimorphism expressed in a molluscan embryo. Embryonic shell dimorphism may provide an early structural template for adult shell dimorphism, permitting females of *M. vorticifera* to store embryos in an enlarged umbilicus, or brood space.

INTRODUCTION

Sexual dimorphism is rare in mollusks (Purchon, 1977). Size rather than shape differences usually produce the dimorphism (Emerson & Feininger, 1972; Webber, 1977), which occurs primarily in higher orders of gastropods. An exception to this pattern is the externally brooding archaeogastropod, *Margarites vorticifera* (Dall). Adults of this boreal-Arctic gastropod exhibit sexual dimorphism associated with a larger umbilical brood space in females (Lindberg & Dobberteen, 1981). Based on Raup's (1966) analysis of shell growth and coiling, Lindberg (1985) determined that shell sexual dimorphism in adult *M. vorticifera* is due mostly to changes in the position of the generating curve relative to the coiling axis. Thus, unlike the majority of gastropods, shell dimorphism in this species is generated by shape rather than overall shell size.

Within the umbilicus of adult females of *Margarites vorticifera* occur brooded embryos in various stages of maturity (Lindberg & Dobberteen, 1981). The most developed of these have early teleoconch shells produced before the embryo is released as a juvenile. In planktonic species, teleoconch shells are a post-metamorphic phenomenon marking the onset of the adult growth phase. Since the teleoconch is typically an adult rather than larval feature, it may be that embryos of *M. vorticifera* express other adult traits while still confined to the brood space. Shell sexual dimorphism (Lindberg, 1985) is perhaps the most biologically significant feature seen in adults of this species. In the present study, we test the hypothesis that shell dimorphism is expressed even in embryonic stages of *M. vorticifera*.

MATERIALS AND METHODS

Adults of *Margarites vorticifera* were collected from 7 m depth near Middle Rocks, Chichagof Harbor, Attu Island, Alaska, U.S.A., in the summer of 1979. Broods were stored in 75% ethanol and later categorized into differential developmental states as reported by Lindberg & Dobberteen (1981). Embryonic (brooded) shells used in this study were from the largest size class of embryos, averaging about 650 μm in diameter. These embryos displayed protoconchs, the beginning of adult shell growth (teleoconch) and ornamentation (Fig. 1).

Our terminology for embryonic and larval shell characteristics follows that of Jablonski & Lutz (1980). The protoconch is the entire shell formed before metamorphosis. Protoconch I is the initial embryonic

shell, while protoconch II is the portion of shell formed during the veliger or planktonic phase. The teleoconch is the post-larval shell laid down after metamorphosis. Applied to brooded embryos of *Margarites vorticifera*, initial shell growth corresponds to protoconch I while the remaining shell (onset of adult phase) is designated as teleoconch, even though it develops while the embryo is still within the brood space (Fig. 1). There is no planktonic phase in this species. Consistent with Giese & Pearse (1974), we consider all the young in the brood to be embryos, including those with teleoconchs.

Shells were cleaned for scanning electron microscopy by bleaching twice for 24 hrs in undiluted Clorox. A distilled water rinse followed each bleaching. After the second rinse, specimens were air dried and mounted on stubs. Mounted shells were coated with gold and viewed with a JEOLCO JSM-2. Stereomicroscopy was used to visualize the coil axis and aperture lip (Fig. 2). Stereo-pairs were produced by tilting the specimen between exposure (Goldstein et al., 1981). Thirty stereo-pairs were used for analysis (Table 1).

To determine parameters associated with development of embryonic shell morphology, four measurements were made from each stereo-pair, using a topographic mirror stereoscope (Fig. 2): the distance from coiling axis to outside aperture edge (D1); the distance from inside aperture edge to outside edge (D2); length of protoconch-teleoconch suture (P1); and the distance from inside edge to outside edge when taken at 85° from the suture (P2). The angle of 85° was chosen because it provided a consistent traverse of the aperture between P1 and P2 (Fig. 2). From these data, three other parameters were derived (Fig. 2 and Table 1): distance from coiling axis to inside aperture lip (D3); ratio of D3/D1 (ratio A); and ratio of D2/D1 (ratio B).

Data used in multivariate analysis are presented in Table 1. To determine the number of groups or types of shell, data were first subjected to the cluster analysis program from the Statistical Analysis System (SAS Inst., 1979). Clustering was based on Euclidian distance. Once the existence of two separate groups was established, a discriminant function analysis (Nie et al., 1975) was used to uncover those parameters most important in distinguishing between the groups. The program also compared classification results of the cluster analysis with the predicted assignments for each shell.

RESULTS

Sixty embryonic shells were examined. Most of these appeared identical in the amount of teleoconch shell growth exhibited and in shell surface ornamentation. A protoconch II phase occurred in roughly 70% of the sample (Fig. 1). Occasionally (6% of sample), shell ornamentation in the protoconch I region differs from that shown in Fig. 1. Instead of bearing a reticulum of fine riblets, these shells have a coarse, granulated surface. This anomaly has no apparent effect on subsequent growth of the teleoconch phase.

After visual study of the stereomicrographs, two shell forms began to emerge. Grouping is based on shape and relative angle of the inside aperture lip (Figs. 2-4). This is the future umbilical area of adults. With visual inspection, roughly two-thirds of the shells could be assigned into one of two groups. Members of one group have a weakly coiled aperture lip which slopes gently toward the coiling axis (Figs. 3A, 4A). The second group comprises shells with a tighter coil and more pronounced slope in this lip area (Figs. 3B, 4B). The more open coiling and gradual sloping lip found in group one produces a larger umbilical space under the ventral surface of the shell (Fig. 3A). To quantify this assessment, as well as to classify the remaining one-third of the sample, data collected from 30 shells (Table 1) were subjected to multivariate statistical analysis.

Existence of two shell groups is confirmed by cluster analysis (Fig. 5). The first group, with 17 members (57% of sample) has higher means for all parameters except P1 and ratio B than does group two. The second group is composed of 13 members, or 43% of the sample. A Student's t-test was performed on the means of parameters for both groups. Means for D1, D2, P2 and D3 (Table 1) all differed significantly ($p < .05$) between group one and group two. Table 1 was arranged after group assignments had been determined, allowing specimens to be listed within their respective group.

The canonical discrimination function, comprised of D1 and ratio B (Fig. 2 and Table 1), accounts for 86% of the variance between the two groups (Table 2). The other parameters listed in Table 1 provide much lower discriminating power, based on selection criteria of

FIG. 1. Embryonic shell of *Margarites vorticifera*. A zone (arrow) similar to protoconch II of planktonic larvae occurs between reticulated protoconch I and the ridged teleoconch. Scale bar = 200 μm.

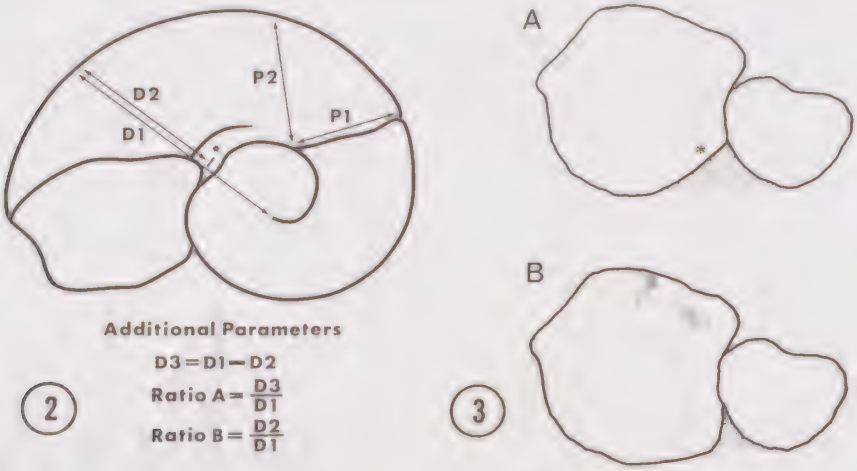


FIG. 2. Shell parameters measured and derived for statistical analyses. Asterisk (*) denotes the aperture lip. Angle between P1 and P2 is 85°. Position of the generating curve is reflected in D1. FIG. 3. Schematic cross section of embryonic shell showing the results of dimorphism. In A, the open coiling and gradual slope of the ventral lip area (*) produce a large umbilical space (shading) relative to that produced by the tightly coiled and sharply sloping lip area in B. A, group one (putative females); B, group two (putative males). Plane of section runs parallel to D1 and through the asterisk of Fig. 2.

Wilks' Lambda, and thus are excluded from analysis. Parameter D1 is about three times more important than ratio B in discriminating between the two groups of shells (Table 2).

Discriminant function coefficients for D1 and ratio B are positive, suggesting that the

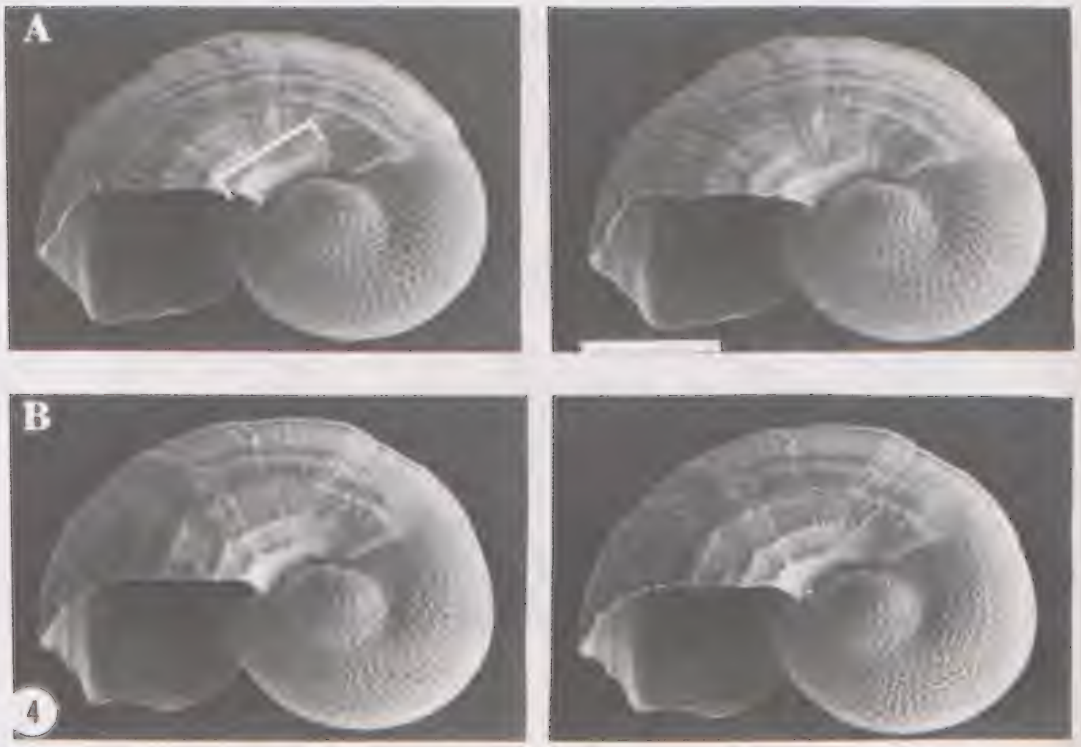
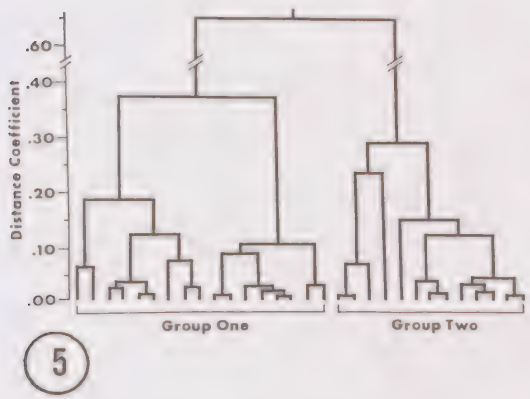


FIG. 4. Stereomicrographs of the ventral shell surface, illustrating shell dimorphism. Viewed with stereoscopic glasses, the coiling described by the lip area (bracket) of A is more open, less curved, than that seen in B. In addition, the lip area of A slopes gradually toward the coiling axis while that of B has a sharper slope. **A**, group one (putative females with larger umbilical space beneath the shell); **B**, group two (putative males). Scale bar = 200 μm.



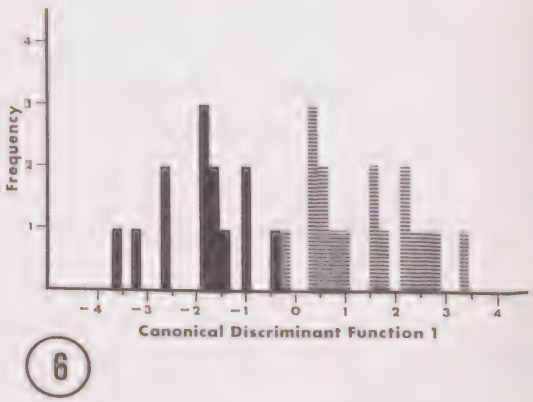


FIG. 5. Results of cluster analysis presented as a dendrogram. Linkage between clusters was derived from the hierarchial agglomerative clustering method. Shells (n = 30) cluster into two groups. FIG. 6. Histogram of individual discriminant scores from discriminant function analysis. Group one (stripes) separates from group two (solid) without overlap.

TABLE 1. Data and parameters used in cluster and discriminant analyses (integers in μm).

Specimen	D1	D2	P1	P2	D3	ratio A	ratio B
1	487	278	187	213	204	.429	.571
2	478	278	183	235	200	.418	.582
3	487	287	174	235	200	.411	.584
4	491	296	165	257	195	.398	.602
5	496	291	165	244	205	.412	.588
6	478	283	178	257	195	.409	.591
7	483	287	196	230	196	.465	.595
8	491	287	161	235	204	.416	.584
9	478	283	170	226	195	.409	.591
10	474	278	187	230	190	.413	.587
11	474	270	187	235	204	.431	.569
12	478	278	187	230	200	.418	.582
13	496	296	178	226	200	.404	.597
14	496	283	165	235	213	.430	.570
15	487	287	200	235	200	.411	.589
16	487	278	165	244	209	.429	.571
17	478	274	183	222	304	.427	.573
18	470	278	200	230	192	.407	.593
19	452	265	174	209	187	.414	.587
20	465	279	196	230	187	.402	.598
21	470	291	174	235	179	.380	.620
22	470	274	200	244	191	.411	.589
23	465	278	187	226	187	.401	.598
24	465	278	191	239	192	.407	.593
25	470	270	191	222	200	.426	.574
26	461	278	183	226	183	.396	.604
27	452	270	209	235	182	.404	.596
28	461	265	191	235	196	.425	.571
29	461	278	191	239	183	.396	.604
30	461	265	187	222	196	.425	.576

differences between groups one and two are due to the value of D1 and ratio B, rather than overall shell size. The frequency histogram of individual discriminant scores shows a clear separation of the two groups with no overlap (Fig. 6). The classification portion of discriminant analysis, based on measured parameters (Fig. 2) and cluster analysis specification, revealed that 100% of the shells were classified correctly.

TABLE 2. Standardized canonical discriminant function coefficients.

Function	Canonical correlation	Parameter	
		D1	ratio B
1	0.8634	0.9860	0.3839

DISCUSSION

Two morphologically distinct groups of shells are found in embryos of *Margarites vorticifera*. Stereoimages (Fig. 4) were superior to conventional micrographs (Fig. 1) in allowing us to determine the degree of coiling and of slope to the inside aperture lip (Figs. 3, 4). About half of the shells coiled tightly and sloped sharply in this region (Fig. 4B), while the other half had a straighter lip which sloped more gradually toward the coiling axis (Fig. 4A). This established a definite, albeit qualitative, dimorphism. To document embryonic shell dimorphism in quantitative terms, we returned to the stereomicrographs to collect data for use in statistical analysis.

Multivariate analysis confirmed the existence of two shell forms among *Margarites vorticifera* embryos (Figs. 5, 6). Each shell was successfully assigned to a group, and there was a 57/42 proportion between groups (Fig. 5). In contrast, visual inspection failed to classify about 35% of the sample. This is due in part to the subtlety of shell dimorphism expressed at such an early developmental stage. That tenuousness is not surprising since detection of some aspects of shell dimorphism even in sexually mature adults requires multivariate analysis (Lindberg, 1985).

Statistical analysis allowed us to uncover two developmental markers, based on shell structure, which could not be detected by visual inspection alone. These are parameters D1 and ratio B (Fig. 2), which were the most consistent criteria for placing embryo shells into one of two groups (Table 2). In Raup's (1966) application of coiling models to gastropods, four parameters were used to describe and predict shell geometry: whorl expansion rate (rate of aperture dilation); whorl translation (along the vertical plane); shape of the generating curve (outline of growing edge of shell); and expansion rate of the generating curve. The latter, referred to by Raup (1966) as position of the generating curve in relation to the coiling axis, is largely accountable for shell sexual dimorphism in adult *Margarites vorticifera* (Lindberg, 1985). Changes in whorl expansion rate also contribute to adult shell dimorphism, though to a lesser extent (Lindberg, 1985). For embryonic shells, we sought parameters (Fig. 2) based on those known to be useful in assessing adult shell morphology.

As in adults (Lindberg, 1985), dimorphism in embryo shells is determined by position of the generating curve in relation to the coiling axis. Parameter D1 is three times more important in establishing dimorphism than is ratio B (Table 2). Parameter D1 reflects the position of the generating curve because as the distance from generating curve (aperture edge) to coiling axis increases, so does the value for D1. Position of the generating curve relative to the coiling axis was also examined using ratio B. Shells with a tighter coil will produce larger values for ratio B than will shells with a more open coil. It would seem that ratio A as well as B should reflect the change in shape with increasing size found in gastropods. However, ratio B is far more important in establishing the existence of two groups of embryonic shells. Arithmetically, this is because ratio B contains a relatively constant numerator whereas both numerator and denominator of ratio A tend to vary in the same direction, decreasing divergence between the two. These ratios are analagous to those recently used by Lindberg (1985) in discriminant function analysis of adult shells.

Discriminant analysis allowed us to statistically distinguish between two groups of embryonic shells (Fig. 5). Among the characteristics in which the groups were expected to differ, parameters D1 and ratio B were the most important (Table 2) in discriminating between groups. To verify the adequacy of our analysis, we returned to the specimens and tested how many were correctly classified solely on the basis of D1 and ratio B. That all specimens were correctly classified (Fig. 6) confirms the existence of shell dimorphism and that it is based on the two parameters discovered by discriminant analysis. Similar use of two types of multivariate analyses has been made by Shin (1982).

Shell dimorphism has not been previously reported for either larval or embryonic gastropods. The phenomenon may exist in other species whose adults, like those of *Margarites*

vorticifera, exhibit a shape rather than size dimorphism. In keeping with D'Arcy Thompson's (1942) idea of logarithmic spiral growth in gastropods, it comes as no surprise that shell dimorphism begins early in ontogeny. Because of logarithmic epigenesis, the progressive changes during early shell development are orders of magnitude smaller than those found in adults. In our study, multivariate analysis was needed to reliably detect embryonic dimorphism. There is no reason to believe that it could not also be found in other dimorphic gastropods such as *Tricolia* (Robertson, 1971), *Ficus* (Arakawa & Hayashi, 1972), and *Marisa* (Demian & Ibrahim, 1972).

In adults of *Margarites vorticifera*, shell dimorphism is associated with increased umbilical brood space in females (Lindberg & Dobberteen, 1981). In our study of embryonic stages, dimorphism is apparent only when **ventral** shell surfaces are viewed (Fig. 4). Embryonic shell dimorphism could be the early expression of two allometries, one of which produces shells better able to accommodate embryo storage as adults. Although embryonic shells could not be sexed, the future sex of group one (Table 1) is probably female. The position of their generating curve foreshadows adult shells with more open coiling, a female characteristic in *M. vorticifera* (Lindberg, 1985). Open coiling creates a larger space beneath the shell (Fig. 3A). In adult females, this space is used to brood the young.

Embryonic shell dimorphism demonstrated in this paper can be used to decipher further the mechanism of development in brooders. Adult dimorphism must occur either as an extension of embryonic dimorphism, or from a qualitatively different phase of shell development which later comes into play. To choose between those alternatives, allometric plots could be used (Gould, 1977; Vermeij, 1980). Plotted between logarithmic axes, the allometry (correlative growth) of shells will be linear with a given slope. Lines of similar slope indicate similar allometries. If the slope of embryonic allometry equals that of the adult plot, embryo dimorphism is an early expression of developmental differences found in adults. Embryos would differ from adults primarily in their size rather than mechanism of development. On the other hand, plots differing in slope would indicate that a different ontogenetic pathway is taken by embryos than by adults.

ACKNOWLEDGEMENTS

We thank D.R. Lindberg for providing specimens for analysis and for participating in many useful discussions, along with J.S. Pearse and D. Jablonski. We are indebted to the late J. Nowell for use of the electron microscope facilities at the University of California, Santa Cruz. This paper is a revised portion of R.A.D.'s senior thesis in biology at the University of California, Santa Cruz. Financial assistance was provided by the Biology Board of Studies, University of California, Santa Cruz. Voucher specimens (cat. no. 29500) are deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

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Malacological Review, 1986, 19: 53-60

CHROMOSOME STUDIES IN THREE SPECIES OF THE GASTROPOD SUPERFAMILY LITTORINOIDEA

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ABSTRACT

The haploid chromosome numbers, as shown by spermatocyte bivalents, are n = 16 for *Littorina punctata*, and n = 13 and n = 14 for *Pomatias elegans* and *P. sulcatus*, respectively. For the latter two species, the diploid chromosome numbers 2n = 26 and 2n = 28 have been observed. No sex chromosomes were found. A comparison between spermatocyte bivalents, as well as their karyotypes, indicates that *P. elegans* may be more evolved than *P. sulcatus*.

INTRODUCTION

Cytogenetic studies are a favored method for clarifying phylogenetic relationships and mechanisms of chromosomal evolution relevant to speciation in closely related species. The karyotypic diversity observed in molluscs makes this phylum particularly suited to this type of research (Burch, 1967; Patterson, 1973; Patterson & Burch, 1978).

In the present investigation, we compared the karyotypes of *Pomatias elegans* (n = 13; Rainer, 1967) and *P. sulcatus* (Gastropoda: Prosobranchia: Littorinoidea: Pomatiasidae), and we discuss some cytotaxonomic aspects which might be derived from our results. In addition, we analyzed spermatocyte bivalents of the two pomatiasid species along with those of the littorinid *Littorina punctata*, also a member of the Littorinoidea.

Information on the chromosomes of this superfamily are rather scanty, because most of the data from the literature refers only to the number and morphology of meiotic chromosomes. These data, briefly summarized in Table 1, indicate that the haploid number n = 13 (Rainer, 1967) is present in both previously analyzed species of the family Pomatiasidae, whereas values ranging from n = 15 to n = 18 have been observed in the family Littorinidae (Nishikawa, 1962; Thiriot-Quievreux & Ayraud, 1982; Janson, 1983; Vitturi & Catalano, 1984).

TABLE 1. Chromosome numbers of nine species of the superfamily Littorinoidea.

Species	n	2n	Source	Reference
Order Mesogastropoda				
Superfamily Littorinoidea				
Family Pomatiasidae				
Pomatias elegans	13		Europe	Rainer, 1967
Pomatias costulatus hyreanus	13		Europe	Rainer, 1967
Family Littorinidae				
Nodilittorina picta	15		Japan	Nishikawa, 1962
Nodilittorina granularis	18		Japan	Nishikawa, 1962
Littoraria strigata	17		Japan	Nishikawa, 1962
Littorina brevicula	17		Japan	Nishikawa, 1962
Littorina neritoides	17	34	France	Thiriot-Quievreux & Ayraud, 1962
Littorina neritoides	16		Italy	Vitturi & Catalano, 1984
Littorina saxatilis		34	Sweden	Janson, 1983
Littorina obtusata		34	Sweden	Janson, 1983

MATERIALS AND METHODS

The following material was employed: 30 male specimens of *Littorina punctata*, from the Gulf of Castellammare del Golfo; 40 males of *Pomatias elegans* (Fig. 1) from the fields near Palermo; and 20 males of *P. sulcatus* (Fig. 2) from the fields near San Vito lo Capo (Sicily). The latter two species differ from each other mainly in the following characters: (1) the shell's color – grey in *P. elegans*, orange in *P. sulcatus*; (2) the outer lip – with a thin and sharp margin in *P. elegans*, thickened in *P. sulcatus*; (3) whorls – more indented in *P. sulcatus*.

The techniques employed for meiotic chromosome preparations are those described elsewhere for other molluscan species (Vitturi et al., 1982). In order to obtain mitotic chromosomes, testes of some specimens were treated before squashing with 0.025% colchicine in double distilled water for 20 min.

Observations and microphotographs were made with a Wild phase-contrast microscope. Mitotic chromosomes were classified according to arm ratio, as proposed by Levan et al. (1964).

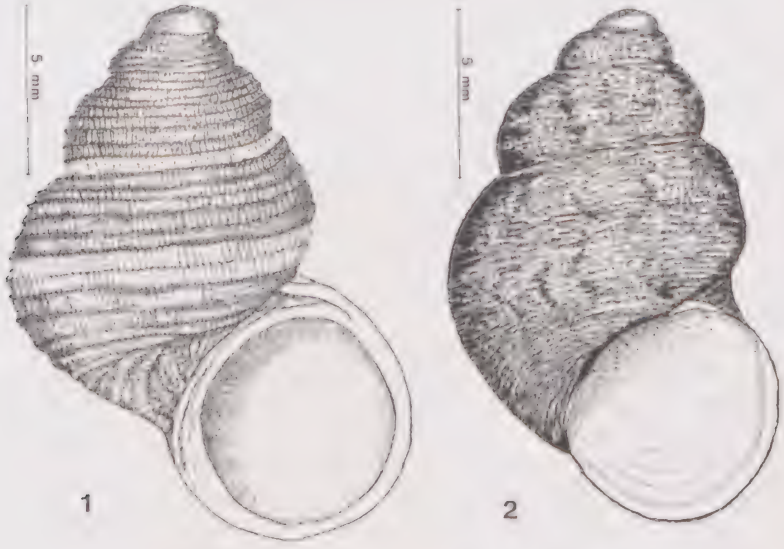

FIG. 1. *Pomatias elegans*. FIG. 2. *P. sulcatus*.

RESULTS

Littorina punctata (Gmelin)

Spermatocyte bivalents were observed at pachytene stage (Fig. 3) and at diakinesis (Fig. 4). Pachytene chromosomes showed an irregular outline; homologues could not be distinguished from each other.

The haploid number was n = 16 in 15 out of 18 plates observed.

This value has been confirmed from the counts of the bivalents at diakinesis (Table 2). At this stage, ring- and cross-shaped chromosomes formed two terminal and subterminal chiasmata respectively. The rod-like morphology did not allow to hypothesize the presence and the position of chiasmata.

The lengths of these bivalents ranged from about 3.2 μm to 1.8 μm.

Pomatias elegans (Müller)

Pachytene chromosomes (Fig. 5) had an irregular outline. Many elements showed partial overlapping on account of a random distribution on the squashing plane. The haploid number n = 13 has been determined with some reserve. At early diakinesis we observed ring-cross- and rod-shaped bivalents (Fig. 6; arrow indicates premetaphase stretch). At late

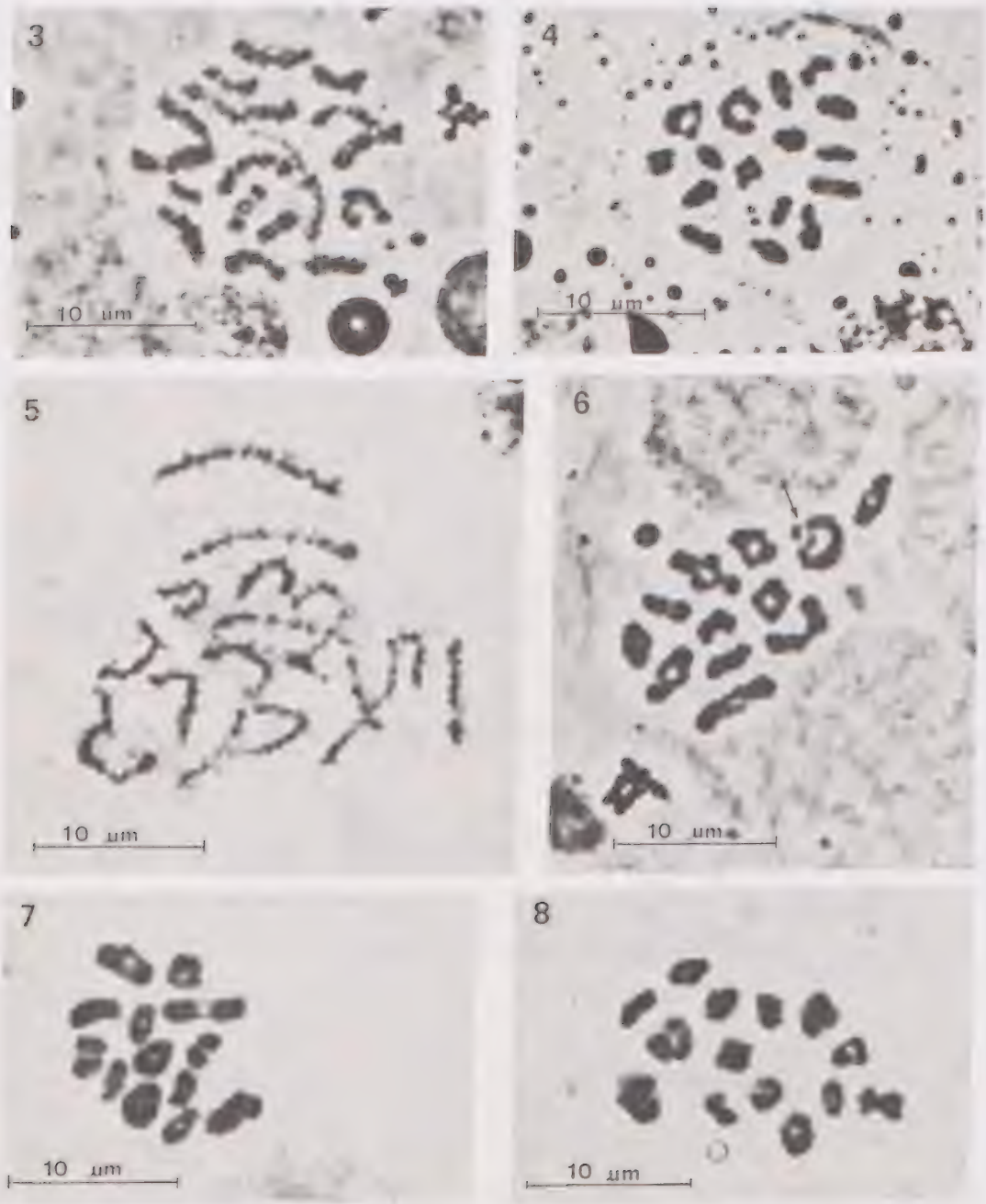

FIG. 3. Pachytene chromosomes in male gonads of *Littorina punctata*. FIG. 4. Diakinetic bivalents in male gonads of *L. punctata*. FIG. 5. Pachytene chromosomes in male gonads of *Pomatias elegans*. FIG. 6. Early diakinesis in male gonads of *P. elegans*. FIG. 7. Late diakinesis in male gonads of *P. elegans*. FIG. 8. Diakinetic bivalents in male gonads of *P. sulcatus*.

diakinesis (Fig. 7) all the elements were homogenously stained and further condensed. The haploid number n = 13 has been determined with certainty (Table 2). The dimensions ranged

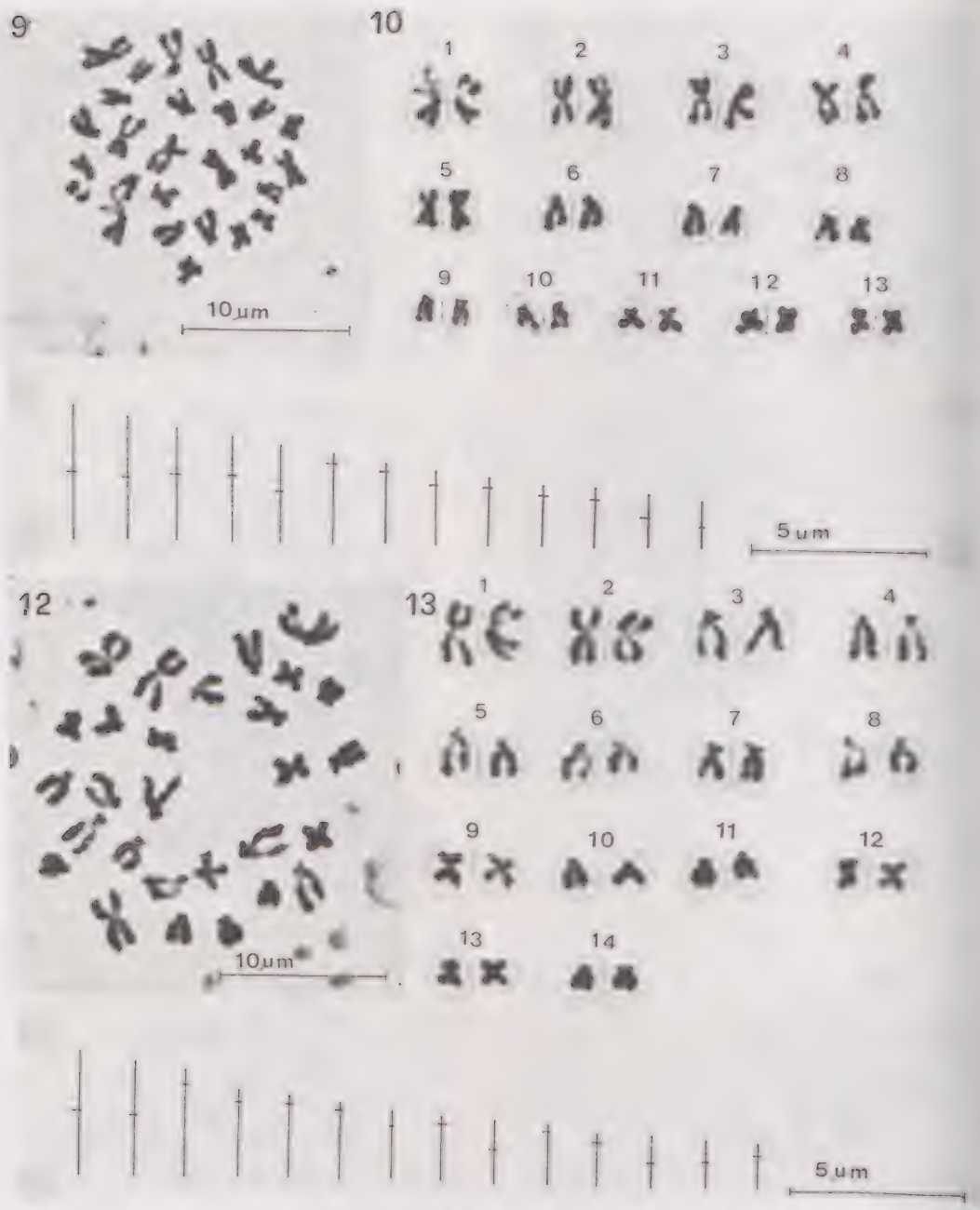

FIG. 9. Spermatogonial metaphase plate of *Pomatias elegans*. FIG. 10. Representative karyotype of *P. elegans*. FIG. 11. Average karyotype obtained from five metaphase plates of *P. elegans*. FIG. 12. Spermatogonial metaphase plate of *P. sulcatus*. FIG. 13. Representative karyotype of *P. sulcatus*. FIG. 14. Average karyotype obtained from five metaphase plates of *P. sulcatus*.

from 5.4 to 2.7 µm at early diakinesis, and from 4.5 to 2 µm at late diakinesis. Spermatogonial metaphase chromosomes also were observed. They appeared randomly scattered on the squashing plane and centromere position was visible in each chromosome (Fig. 9). The diploid number was 2n = 26 (Table 2).

TABLE 2. Chromosome numbers of three species of the superfamily Littorinoidea.

Littorina punctata	Haploid numbers	14	15	16	17	18
	Frequences	3	5	42	2	
Pomatias elegans	Haploid numbers	11	12	13	14	15
	Frequences	4	7	65	3	1
	Diploid numbers	24	25	26	27	28
	Frequences	2	8	22	1	2
Pomatias sulcatus	Haploid numbers	12	13	14	15	16
	Frequences	1	4	36		2
	Diploid numbers	26	27	28	29	30
	Frequences	5	9	38	3	3

Five sets were tentatively arranged into pairs according to decreasing size (Fig. 10; one plate is represented). Total measured length of these chromosomes, arm ratio and general morphological appearance, as observed in the photographic prints, were the criteria used for pairing. The average karyotype (Fig. 11) showed that *Pomatias elegans* possessed 13 pairs of autosomes, seven of which were metacentric, six subtelocentric and acrocentric (Table 3).

TABLE 3. Mean length and arm ratio of the chromosomes of five mitotic metaphase plates of *Pomatias elegans* and *P. sulcatus*.

Pomatias elegans													
Chromosome pairs	1	2	3	4	5	6	7	8	9	10	11	12	13
Mean length (μ)	4.18	3.77	3.50	3.31	3.00	2.77	2.54	2.27	2.15	1.97	1.86	1.72	1.57
Standard deviation	0.67	0.70	0.70	0.56	0.51	0.56	0.49	0.48	0.54	0.45	0.37	0.37	0.25
Arm ratio (mean)	1.04	1.07	1.48	1.70	1.17	7.24	7.75	3.62	8.11	6.48	3.10	1.06	1.00
Centromere position	M	M	M	M	M	A	A	ST	A	ST	ST	M	M
Pomatias sulcatus													
Chromosome pairs	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Mean length (μ)	3.90	3.50	3.27	2.72	2.54	2.31	2.22	2.13	2.00	1.93	1.72	1.72	1.54	1.45
Standard deviation	0.51	0.37	0.20	0.00	0.19	0.19	0.19	0.25	0.19	0.27	0.12	0.12	0.10	0.12
Arm ratio (mean)	1.07	1.00	5.92	5.66	7.48	10	3.90	7.10	1.05	6.60	5.33	1.00	1.07	2.55
Centromere position	M	M	ST	ST	A	A	ST	A	M	ST	ST	M	M	SM

Pomatias sulcatus (Draparnaud)

Diakinetic bivalents (Fig. 8) of *Pomatias sulcatus* were similar to those of *P. elegans*: in fact, ring-, cross- and rod-shaped elements were present. The haploid (n = 14) and the diploid (2n = 28) values have been determined (Table 2). The dimensions of dikinetic bivalents ranged from 3.2 to 2 μm.

The average karyotype (Fig. 14) constructed from five sets (Figs. 12, 13; one plate is represented) showed the presence of 14 pairs of autosomes, six of which were metacentric and submetacentric, eight subtelocentric and acrocentric (Table 3).

DISCUSSION

By counting spermatocyte bivalents, we have determined the haploid number of chromosomes n = 16 for *Littorina punctata*, and n = 13 and n = 14 for *Pomatias elegans* and *P. sulcatus*, respectively. Diploid numbers of 2n = 26 and 2n = 28 obtained from counts of spermatogonial metaphase spreads have confirmed the corresponding haploid numbers for the latter two species.

On the whole, chromosomes of the species analyzed in this study are very similar to those of many other molluscan species. More precisely: (1) pachytene bivalents resemble "lumpbrush chromosomes" (Vitturi, 1982; Vitturi & Catalano, 1984); (2) some spermatocyte bivalents bear chiasmata. Of course, it is very likely that not all the chiasmata were identified, since these chromosomes were not observed at the diplotene stage; (3) an XY sex-determining mechanism seems to be absent in *Pomatias elegans* and *P. sulcatus* as no heterotypic element occurs in the diakinetic and spermatogonial metaphasic plates investigated here. On the other hand, differentiated sex chromosomes within the class Gastropoda have been noted in two species of *Pomatiopsis* (Burch, 1960; Patterson, 1963), in the family Viviparidae (Patterson, 1965; Stern, 1975) and in the species *Rissoa ventricosa* (Mesogastropoda) (Thiriot-Quievroux & Ayraud, 1982).

Distant somatic pairing between similar chromosomes in spermatogonial metaphase plates is considered to be a very common character in the animal kingdom (Kitani, 1964; Colombera, 1970). This phenomenon has not been noted in *Pomatias elegans* nor in *P. sulcatus*. In fact, their mitotic metaphase chromosomes appear randomly distributed on the squashing plane, as observed in *Bursatella leachi savignana*, *B. leachi leachi* (Opisthobranchia) (Vitturi et al., 1985b) and in *Teredo utriculus* (Pelecypoda) (Vitturi et al., 1983).

The lack of conservatism in the chromosome number, not only within the families Pomatiasidae and Littorinidae, but also within the genera *Pomatias* and *Littorina*, is apparent, because the haploid numbers n = 14 and n = 16 have been found in *P. sulcatus* and in *L. punctata*, respectively (Table 1).

As *Pomatias elegans* and *P. sulcatus* are morphologically closely related species (Giusti & Castagnolo, 1982), one would expect to observe chromosomal similarities among them. On the contrary, they differ not only in chromosome number but also in karyotype. In particular, we find 13 and 14 bivalents in *P. elegans* and *P. sulcatus*, respectively. Moreover, we can observe that there is not a complete relationship between morphologically similar chromosomes in two karyotypes. This evidence is clearly supported if we compare the first five pairs of chromosomes: they are all metacentric in *P. elegans*; they are metacentric, subtelocentric and acrocentric in *P. sulcatus* (Table 3).

Interestingly, both species under study show the same fundamental number (NF = 20) and a very similar appearance in size of karyotypic chromosome pairs. It leads to the supposition that differences between the two karyotypes might be due to those mechanisms which are thought to be responsible mainly for chromosomal rearrangements, such as Robertsonian fusion and pericentric inversion.

Our work is in progress to develop G-banding techniques for these snails, and we hope that changes in centromere position within the genus *Pomatias* may soon be known in great detail.

Finally, some authors have suggested that evolution in general (Mayr, 1970; Colombera & Lazzaretto-Colombera, 1978) and inside molluscs in particular (Vitturi et al., 1982; Vitturi et al., 1985a) is accompanied by a decrease in the chromosome numbers. Furthermore, it is believed that ancestral karyotypes appear to be less symmetrical than those observed in specialized species (Ohno, 1970; Colombera & Vitturi, 1978; Dingerkus, 1979; Sharma & Agarwal, 1981). If these hypotheses are correct, it would seem that *Pomatias elegans* is more evolved. In fact, *P. elegans* exhibits a haploid set of 13 chromosomes, as well as a more symmetrical complement than that observed in *P. sulcatus*.

ACKNOWLEDGMENTS

The authors are deeply indebted to Mr. G. Miceli for processing and printing the microphotographs presented here, and to Dr. G. Barbata for the English revision of the manuscript.

This research was supported by grant: ricerca scientifica bilancio 60%, 1984.

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Malacological Review, 1986, 19: 61-81

THE APPLE SNAILS OF THAILAND: DISTRIBUTION, HABITATS AND SHELL MORPHOLOGY

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ABSTRACT

According to morphological characters, supported by genetic analyses and aspects of anatomy, the freshwater snail genus *Pila* in Thailand has five species: *P. ampullacea, P. angelica, P. gracilis, P. pesmei* and *P. polita*. Of these species, *P. ampullacea* and *P. polita* are the most easily distinguished morphologically. *Pila ampullacea* has a white or purplish-white lip; *P. polita* has a very shiny and oval shell. The other three species are very similar morphologically, which can cause recognition problems. *Pila gracilis* can be misidentified as the small form of *P. pesmei*, and *P. angelica* can be misidentified as the large form of *P. pesmei*. The shells of these latter three species all have a very similar appearance, which includes their yellowish-orange apertural lips and banded shells.

Pila gracilis and *P. polita* are closely related and share common features such as the ovate-conical shell shape, yellowish-orange lip and thin, steel-blue nacre of the operculum. However, the two species show anatomical differences. *Pila ampullacea, P. angelica* and *P. pesmei* are closely related and similar in their globosely conic shell shape. *Pila angelica* is more closely related to *P. pesmei* than it is to *P. ampullacea*. The common features that both *P. angelica* and *P. pesmei* share are the large, globose, banded shell and yellowish-orange lip. The shell features, apart from the anatomical structures, that show *P. angelica* to be a different species from *P. pesmei* are the color of the nacre of the operculum and the thickness of the shell. *Pila angelica* has a thin shell and steel-blue nacre on the operculum. *Pila pesmei* has a thick shell and silvery pinkish-white nacre.

Pila pesmei shows much genetic variability in regard to shell characteristics. The shell size ranges from medium to large. The shell form is also variable, which in some specimens is like *P. angelica*, in others is similar to *P. gracilis*.

Pila ampullacea is closely related to *P. pesmei*, sharing common features, such as the silvery-pinkish white color of the nacre of the operculum and the well-rounded, globose-shaped shell. *Pila ampullacea* is not widely distributed. Small specimens of *P. angelica* are very similar to young *P. ampullacea*, but *P. ampullacea* has a long cylindrical renal vas deferens and its distribution does not overlap with *P. angelica*. *Pila ampullacea* occurs in central, northern and northeastern Thailand, while *P. angelica* is found only in the south.

Pila "scutata", considered by previous authors to be a good species, is merely a rare non-banded form of *P. gracilis*.

INTRODUCTION AND HISTORICAL REVIEW

Species of the gastropod family Pilidae (Ampullariidae), commonly known as "apple snails" because of their large size and globose shape, are found in tropical fresh waters throughout the world. In Thailand, the family is represented by the single genus *Pila*, which is widely spread and often very abundant. Its species are common in rice fields and shallow bodies of water with succulent vegetation, which provides places for shelter. These aquatic plants can provide food for the snails either as fresh vegetation or as decaying humus (Fretter & Graham, 1962).

The economic importance of Thai *Pila* is in providing food for Thais, mostly farmers. These snails are large, abundant, easily found, and the foot tastes good. The snails habitually are eaten raw. However, unfortunately, the consumers are not aware that the snails are intermediate hosts of two important species of parasites infecting humans, *Angiostrongylus cantonensis* Chen and *Echinostoma ilocanum* (Garrison). *Angiostrongylus cantonensis* is a

nematode parasite of rodents. The parasitic larvae must develop in an invertebrate, and can infect species of *Pila*, which, when eaten, transfer the infective larval parasites to the predator, where they continue their development. The presence of the nematode parasites in humans causes angiostrongyliasis (eosinophilic meningoencephalitis), often resulting in death (see Harinasuta et al., 1965). Species of *Pila* are, at present, considered very important mediators to humans of this serious parasitic disease. The second parasite, *E. ilocanum*, is a trematode, an intestinal fluke which lives attached to the wall of the small intestine. This parasite causes inflammation, ulceration, diarrhea and anemia in its human hosts (Faust et al., 1974).

The various species of *Pila* are amphibious, and their respiration may be wholly branchial or entirely by the pulmonary surface of the mantle cavity, depending on whether the snails are in or out of the water. In the dry season, the snails can bury themselves in the ground, where they remain in a comatose condition, with the operculum tightly sealing the aperture of the shell. Because they were found in the ground during dry seasons, Linnaeus may have wrongly regarded the Pilidae as terrestrial in his original description of the first pilid species to be recognized, since he referred *P. ampullacea* to the genus *Helix* (Pain, 1972).

Snails of the genus *Pila* have been known to science since pre-Linnaean times (Michelson, 1961), i.e., prior to the 18th century. Pain (1972) recorded *Pila* as Miocene fossils in Kenya, where the genus is still found living today, indicating considerable longevity, at least in East Africa. The Old World apple snails were given several different generic names in the 18th and 19th centuries: *Pila* Röding 1798, *Ampullaria* Lamarck 1799 and *Pachylabra* Swainson 1840. *Pila* has chronological priority. This genus, restricted to the Old World (i.e., to Eurasia and Africa) is characterized by a calcareous operculum and short siphon (Annandale, 1920).

The shells of the Pilidae worldwide range in size from medium to very large (i.e., from 30 mm to nearly 100 mm), are dextrally coiled (a few are ultra-sinistral), moderately thick to thin, ovate, globose, subglobose or planate in shape, and usually are perforate to broadly umbilicate (rarely the umbilicus is closed). The surface of the shell usually is smooth; rarely there are spiral grooves, carinae or ribs. The operculum is either thin, flexible and corneous, or thick, rigid and calcareous.

By external characters based on color, size and shape of the shell, and the presence or absence of an umbilicus, the family Pilidae as presently classified consists of seven genera. *Pila, Lanistes, Afropomus* and *Saulea* are the Old World genera; *Pomacea, Marisa* and *Asolene* are the New World genera. The Old World genera occur in Africa. *Pila* is also found in Asia. In the New World, *Pomacea* is found in South America, Central America, the West Indies and the southern U.S.A., *Marisa* occurs in South America and the West Indies, and *Asolene* is restricted to South America (Michelson, 1961).

The nature of the respiratory siphon (whether short or long) has been used as a criterion for the separation of Old and New World taxa. *Pila, Lanistes* and *Afropomus* have short siphons; the siphon of *Saulea* has not yet been described. The New World genera, *Pomacea, Marisa* and *Asolene*, have long siphons (Pilsbry & Bequaert, 1927). Prashad (1925b) suggested that the morphology of the siphon reflects an adaptation to ecological conditions and is not of phylogenetic significance.

The eggs of the various species provide characteristic differences which may be of phylogenetic importance. Both *Pila* and *Pomacea*, which are highly and moderately amphibious, respectively, produce calcareous-shelled eggs and deposit the eggs out of water. *Marisa* and *Lanistes* are both aquatic and have gelatinous eggs, which are deposited below the waterline (McMahon et al., 1957). Pilsbry (1933) reported the eggs of *Asolene* to be gelatinous. The eggs of *Saulea* and *Afropomus* have not been described.

The family Pilidae, basically aquatic, seems to have an evolutionary trend towards the terrestrial biotope. Morphological adaptation for the transition from the aquatic to the terrestrial habitat is provided by the animals having a lung in addition to gills. Since the calcareous

eggs of *Pila* and *Pomacea* are deposited out of water, the dependence of the snails on an aquatic habitat is reduced. Both *Pila* and *Pomacea* seem to represent evolutionary advances towards the terrestrial mode of existence.

A modern classification of oriental Pilidae was first undertaken by Annandale (1920) on Thai *Pila*. Annandale described habitats, behavior, radular teeth, eggs, and particularly shell characters (i.e., shell shape, number of whorls, structure of operculum, color, etc.). Even though it was difficult to distinguish snails by using his identification key, he described pertinent details that now can be related to several species of Thai *Pila*.

Annandale and his assistant, Dr. B. Prashad, later (1921) studied Indian Pilidae and based their classification mostly on shell and opercular characters, since the soft parts were still unknown in a majority of the species. Annandale and Prashad mentioned that this family gave systematists a great amount of difficulty. Distinguishable forms occur among a number of species, and some populations exhibit considerable individual variability. In 1921 very little had yet been known of the anatomy of the Pilidae, but it seemed to Annandale and Prashad that both shell characters and radular morphology could demonstrate conspicuous differences among the species. In their study, they reported two new species, *Turbinicola nux* (Reeve) and *Pachylabra nevilliana* Annandale & Prashad, based on shell and opercular characters, and on radular form. Later, Prashad (1925a) divided the Indian Ampullariidae into two genera, *Pila* for the common forms found in the plains and *Turbinicola* for the hill-stream species. He regarded *Pila* to consist of eight species and six varieties, which he described in regard to the shape, thickness, number of whorls, sculpture and color of their shells, and the morphology of their opercula. These characters, as well as geographic distribution, were used as criteria to distinguish the taxa. [Pilsbry & Bequaert (1927) subsequently concluded that both *T. nux* and *P. nevilliana* are conspecific, and belong to the genus *Pila*, i.e., they are merely intraspecific variants.]

Because *Pila globosa* (Swainson) was the common Indian apple snail, it was used for dissection by zoology classes in various universities. Prashad (1925b) published a paper on the anatomy of *P. globosa*, which included general characteristics of the animal and its internal organ systems (i.e., reproductive, respiratory, nervous and digestive systems). His paper contained a complete and very useful account of *P. globosa*.

Another significant report on the Pilidae was that of Pilsbry & Bequaert (1927) in their monograph on the freshwater mollusks of the Belgian Congo. They divided the family into seven genera. They characterized these genera by the position of the aperture (dextral or sinistral), type of operculum (corneous or calcareous), characters of the umbilicus (closed or open), and length of the siphon (short or long). Specific shell characters are those of shape, color, thickness, and sculpture pattern. Pilsbry and Bequaert reported 21 species of African *Pila*, with one subspecies and two varieties. These were characterized by their sculpture, aperture width, and the length of the adnate portion of the inner lip relative to that of the aperture. Because of the difficulty in differentiating the species due to their similarity, most African *Pila* were insufficiently described.

The most recent taxonomic study on the Pilidae using comparative morphology was that of Michelson (1961), who reviewed the generic taxonomy of the family, and studied five genera of the family anatomically (*Pila*, *Lanistes*, *Afropomus*, *Pomacea* and *Marisa*). He concluded that only two structures, the kidney and the penial complex, were morphologically different among the genera.

Only two systematists previously have dealt with Thai *Pila*, Annandale (1920) and Brandt (1974). Annandale recognized seven species and two races for Thailand *Pila* and Brandt recognized five species, without any division into races. Although Brandt's study was recent, he did not look at anatomical characters. His taxonomy was based on shell shape, color and sculpture, and on geographic distributions. Brandt's identification key was used during my study, but even with it the determination of *Pila* proved difficult because of the morphological similarity of the species, and because of intraspecific variability.

My study of Thai *Pila* combined shell characteristics, anatomical systems, distribution and genetics. Neither anatomical studies nor genetic patterns alone can provide a definitive systematics of *Pila* in Thailand. My studies showed on the one hand that two different "species" (i.e., forms showing noticeably different shell characteristics) give the same genetic patterns, and on the other hand that two forms which are very much alike in shell structure give different genetic patterns. The best way, therefore, is to analyze genetic patterns and to correlate these with comparative anatomy and shell morphology. The results of the shell analysis are presented below. The anatomical and genetic studies will be published elsewhere.

MATERIALS AND METHODS

Selection of snail populations

The most recent revision of the Pilidae of Thailand was that of Brandt, who recognized five species, which he included in the single genus *Pila*. Brandt's taxonomy was based exclusively on shell characteristics. Initially, I used Brandt's taxonomic key as a guide to the Thai *Pila*, but I found that several of the species were difficult to distinguish. For example, several populations had shell characters (i.e., shape and color) that did not fit Brandt's key characters. Also, allopatric populations of the same presumable species were sometimes difficult to compare because of shell variation. Therefore, before beginning the collecting program, I had to study shell specimens which were collected from all over the country by staff of the Southeast Asian Center for Applied Malacology and Entomology at Mahidol University in Bangkok. I could then, after studying and discussing the various populations with the staff of the Center, divide the *Pila* populations into six different groups. Then, I selected 11 populations of these six groups in order to study geographic variation between populations. These 11 populations are as follows.

P. ampullacea, Bangkok
P. ampullacea, Chon Buri
P. angelica, Songkhla
P. gracilis, Songkhla
P. gracilis (including *P. "scutata"*), Pattani
P. pesmei, Suphan Buri
P. pesmei, Chon Buri
P. pesmei, Ubon Ratchathani
P. polita, Bangkok
P. polita, Ubon Ratchathani
P. polita, Phayao

Localities for the above populations are shown in Fig. 1. Table 1 gives the distributions of the taxa I recognized compared to the taxa and their distributions as understood by Brandt (1974). Voucher specimens have been deposited in the collections of the Mollusk Division, Museum of Zoology, The University of Michigan.

I selected a specific population found close to Bangkok as a standard with which to compare the other populations, and one which was not too difficult to rear in the laboratory. Thus, this species was constantly available for comparative purposes. The population I selected as a standard was *Pila ampullacea* living in a pool at Kasetsart University, Bangkok. The populations of this species increase in the summer during the months of April, May and June. Then in the following rainy season, which occurs from July to October, the snails are very common. In winter, i.e., during November to February, *P. ampullacea* virtually disappears from water bodies. During this period, the snails aestivate underground.

Collecting, transporting and marking snails

Pila snails were collected with long-handled dipnets and pails. The preferred habitats of the snails are old ponds, pools and marshes which are not too crowded with aquatic vegetation (e.g., water hyacinth and morning glory). A dipnet was used if the snails were floating or attached to plants. If the snails were on the bottom of the body of water, I would go into the water and hand pick them. To transfer the snails from the field to the laboratory, it was not necessary to have water in the pails containing the snails. For long distance transportation, the snails were wiped dry, wrapped in newspaper and placed in a paper box.

After arriving in the laboratory, the snails were wiped dry again and a part of the shell of each specimen was scrubbed and marked with the place and date of collection. A bright colored fingernail enamel was used for marking the shells. The snails from each locality were then divided into three groups. Group

FIG. 1. Localities at which collections were made: 1, Bangkok; 2, Chon Buri; 3, Suphan Buri; 4, Ubon Ratchathani; 5, Phayao; 6, Songkhla; 7, Pattani.

1 was divided into two subgroups: subgroup 1.1 was maintained in the wet laboratory and provided material for electrophoretic studies; subgroup 1.2 was reared in a natural pool in an orchard. Group 2 was induced to aestivate and group 3 was narcotized and preserved [see Keawjam (1986) for details].

Maintenance of snails in the laboratory

Pila ampullacea and other snails that were to be maintained for prolonged periods were kept in large aquaria (40 x 70 cm) that had a mud slope for aestivating and resting. At least 15 large snails were kept in each aquarium. Aged tap water partially filled the aquaria, leaving some of the mud slope above water. Old water was replaced periodically with clean water. Light was provided by a 15-watt cool, white fluorescent tube for 10 hrs each day. Aeration was provided by a line from an air compressor. Temperature in the aquarium room was maintained during 10 hrs of the day at 24-27°C by an air conditioner. In the evening and at night the air conditioner was turned off and the windows were opened to circulate natural

TABLE 1. Comparison of the species of *Pila* and localities of Brandt (1974) with those of the present study.

Brandt's distributions	Keawjam's distributions
P. ampullacea In all Thai provinces except Mae Hongson (in the north).	*P. ampullacea* Common in central Thailand, rare in the north and northeast, never found in the south. *P. angelica* Found only in the south, none in central, northern and northeastern Thailand.
P. gracilis Eastern, southeastern and central Thailand.	*P. gracilis* Common in south of Phanga-nga; none have been found in central, northern and northeastern Thailand.
P. pesmei All over Thailand, except for the provinces south of Yala.	*P. pesmei* Very common in central and northeastern Thailand. Rare in the north; absent from the south.
P. polita In northern, northeastern and eastern Thailand. None occur in the south.	*P. polita* Very common in central, northern and northeastern Thailand. None were found in the south.
P. "scutata" In southern, western and northern Thailand.	*P. "scutata"* Found only in the south and very rare. Found among a population of *P. gracilis*.

air in the room. The snails were fed commercial fishfood flakes, fresh lettuce and diatoms. For more details regarding snail maintenance in the laboratory, see Keawjam (1986).

Habitat characteristics

Species of *Pila* seem to prefer older bodies of water which have aquatic vegetation. The kinds of vegetation present in the habitat were indicative of the density of snails to expect, i.e., ponds having mostly water hyacinth would have more snails than ponds having mostly grass. The plants provided not only shelter and substrate for the snails, but also could be consumed as food. It was, therefore, important to note characteristics of the habitats from which the snails were collected. The natural habitats were photographed and observations were made on details of the snail life histories.

DESCRIPTIVE SHELL MORPHOLOGY, DISTRIBUTION AND HABITATS

General characteristics of the genus *Pila*

Shell medium to large, ovate-conical, oval to globosely conic, dextral, with thin or thick, brown or greenish-brown periostracum; usually perforate, or rarely with umbilicus closed. Surface usually smooth, with transverse growth lines or striae; color markings, if present, of

dark brown streaks or bands. Lip widely or elongately oval, with straight columella. The operculum completely closes the aperture; it is calcareous, concentric, with its nucleus nearer the parietal margin; inner surface nacreous.

Pila ampullacea (Linnaeus 1758)
(Fig. 2)

Shell large, moderately thick, globosely or widely conic, with low, conical or obliquely flat spire whose one or two whorls are often corroded; number of whorls 5½, with body whorl well rounded or evenly convex, upper surface appearing obliquely flattened. Aperture oval, obliquely rounded near the basal lip, width of the mouth about ⅘ of the aperture

FIG. 2. Shells of *Pila ampullacea*. 1, Chon Buri; 2, 3, Bangkok.

height, which was approximately ¾ of the shell length; parietal callus moderately thick and wide, but not as thick and wide as that of *Pila pesmei*; lip sharp, thick and strong, whitish or somewhat purplish-white. Operculum heavy and thick, with the inner surface or nacre silvery pinkish-white. Umbilicus wide and deep, but sometimes covered over by the retroverted inner lip of the mouth. Color of the shell brown or olive-green, unbanded or rarely banded.

Size of full-grown shells: W 45-80 mm; H 55-86 mm.

Distribution: Common in the central part of Thailand, i.e., Bangkok, Nontha Buri, Chachoeng-sao, Prachin Buri, Suphan Buri, Sing Buri and Chon Buri; rare in the northern and northeastern provinces. It never was found in Prachuap- khiri-khan Province or in the south (Fig. 3).

Pila ampullacea inhabits canals in which the water current is not fast, e.g., ditches, swamps

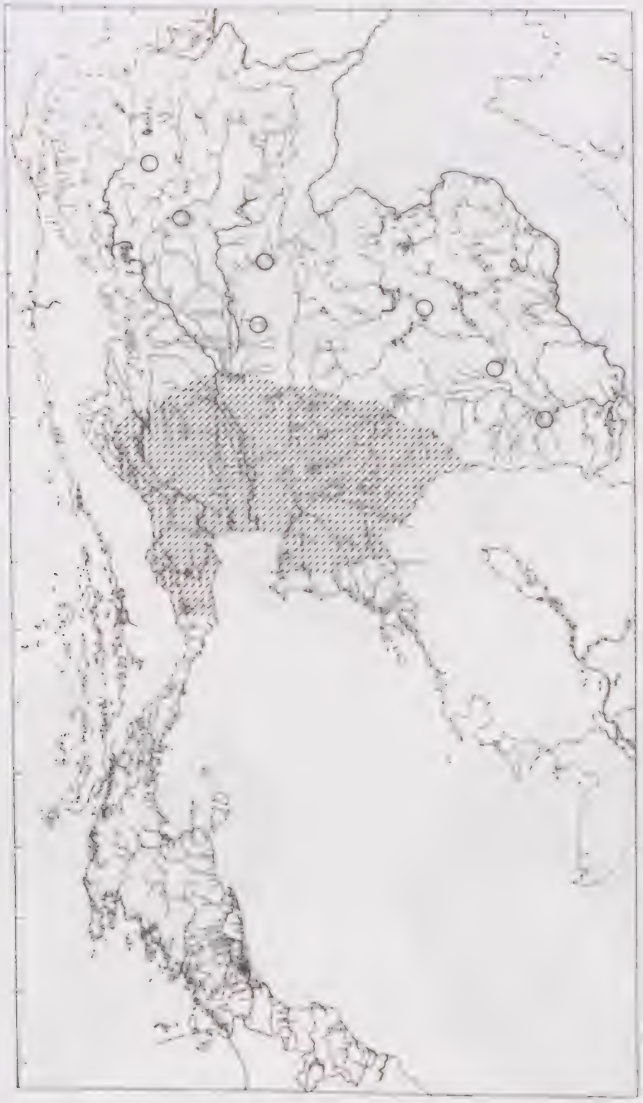

FIG. 3. Distribution of *Pila ampullacea*.

and even irrigation canals. The snails attach mostly to aquatic plants such as water hyacinths, water lilies, morning glories and grasses. They were very common in July through October and were rarely seen from November through March, during which time they probably were aestivating underground. Sometimes, they were found 1-3 ft deep in the hard ground. The snails can aestivate in the laboratory for at least one year. They can be found in the same water bodies as *P. polita* and *P. pesmei*, but the proportion of these three species varies with the season.

Pila angelica (Annandale 1920)
(Fig. 4)

Shell large, widely globose, having a low, flat spire with one or two eroded whorls. Shell

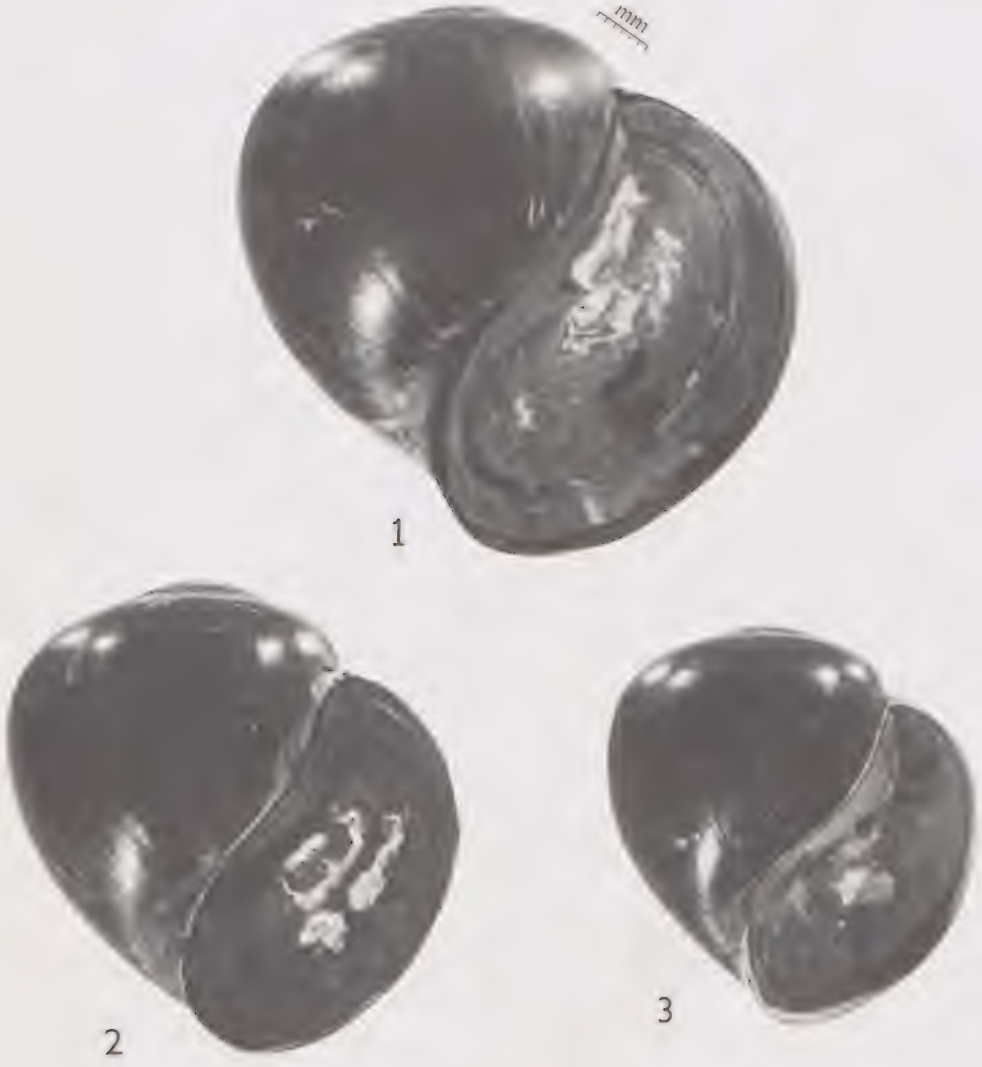

FIG. 4. Shells of *Pila angelica*. 1, Songkhla; 2, 3, Phang-nga.

usually thin, thicker when the animal is extremely large, but never as thick as that of *Pila ampullacea* or *P. pesmei*. Body whorl with narrow smooth shoulder, then rounded, and tapered downward at the basal lip; number of whorls about 4¼. Aperture elongately oval, often with a beak at the basal lip; width of the mouth about half the aperture height (which was higher than ⅔ of the shell length). The upper end of the aperture is shorter in distance below the upper margin of the body whorl than in *P. ampullacea* and *P. pesmei*. Lip sharp, thin, moderately strong, yellowish-orange or greyish-orange, with parietal callus thin and narrow. Operculum rather thin, with steel-blue nacre. Umbilicus somewhat narrow. Color chestnut-brown or greenish-brown with thin darker-brown spiral bands.

Size of full-grown shells: W 50-70 mm; H 60-75 mm.

Distribution: Found only in the southern provinces from Chumphon southward to the southernmost part of the country. Very common in Suratthani, Phang-nga, Songkhla and Pattani (Fig. 5).

FIG. 5. Distribution of *Pila angelica*.

Pila angelica was found in both moving and standing waters. It attached to rocks, logs and aquatic plants, in clear and somewhat rapid mountain streams or creeks. It was also common in brackish lakes. The plants in both habitats were mostly palms, water hyacinths and algae. The snails were most common from April through August. They occupied the same habitats as *P. gracilis*, but they needed higher water levels. *Pila angelica* could be stimulated to aestivate in the laboratory, but not for longer than seven months.

Pila gracilis (Lea 1856)
(Fig. 6)

Shell medium, rarely large, texture thin, ovate-conical or subglobosely conic, with spire little exerted; the one or two spire whorls usually are eroded; number of whorls 4¼; body whorl smoothly sloped at the upper surface, increasingly rounded at the middle, and then evenly tapered downward near the basal lip. Aperture oval, with the mouth angled downward; width of the mouth about half the aperture height (which was not greater than ¾ of the shell length). Lip sharp and thin, somewhat strong, yellow colored, with parietal callus thin and narrow. Operculum thin, with the inner surface nacre steel-blue. Umbilicus very narrow, often covered over by the retroverted inner lip of the aperture. The color of the shell varies with the environments, ranging from chestnut-brown or greenish-brown, with conspicuous darker-brown spiral bands. Unbanded specimens occasionally were found.

Pila "scutata" (Mousson), as identified by Brandt (1974), has shell characteristics very similar to those of *P. gracilis*, except that shells of *P. "scutata"* lack bands. I found only three specimens (two females and one male) of this bandless southern form among the population of 200 *P. gracilis* in rice fields in Pattani, and I found none at Songkhla on my first trip to the south. One month later, on the second trip, I found three bandless specimens (all females) in Songkhla. Six of these *P. "scutata"* were compared electrophoretically to *P. gracilis*. The results obtained were enough to prove to me that both forms belonged to the same species, *P. gracilis*. [The electrophoretic study of Thai *Pila* will be published separately.] Shells without bands are only variants, i.e., they are a non-banded form of *P. gracilis*.

Size of full-grown shells: W 24-38 mm; H 30-46 mm.

Distribution: This species is found only in the southern part of Thailand. It is common in Phang-nga, Phuket, Krabi, Phatthalung, Songkhla, Pattani and Yala, but seems to be rare in the provinces above Phang-nga, such as Surat-thani, Ranong and Chumphon (Fig. 7). It has not been found in the central, northern and northeastern parts of the country.

Pila gracilis is very common in standing waters, and is rare in canals and mountain streams. It is found attached to rice stalks in rice fields or to aquatic plants, i.e., algae, morning glories, grasses and water hyacinths, which grow in the swamps, pools, ditches and ponds. This species often inhabits polluted water in effluent pipes. It is found during the same time periods as *P. angelica*, but needs lower levels of water. *Pila gracilis* could aestivate for only seven months in the laboratory.

Pila pesmei (Morelet 1889)
(Fig. 8)

Shell sizes and characteristics are very variable. Shell medium to large, thick, globosely or widely conic, with a low spire, whose one or two whorls are often eroded; number of whorls 4¼ or rarely 5¼; body whorl well rounded, its upper margin slightly cushioned. Aperture elongately oval, its upper margin a little angled; width of aperture about half its height; height of aperture about ¾ of the shell length; parietal callus thick and wide; lip

FIG. 6. Shells of *Pila gracilis*. 1-3, Songkhla; 4-9, Pattani. Specimen no. 5 is *P. gracilis* (*"scutata"*).

FIG. 7. Distribution of *Pila gracilis*.

thick and slightly retroverted, strong, yellowish-orange. Operculum thick, with silvery pinkish-white nacre. Umbilicus narrow and moderately deep, often covered over by the raised peristome. Color of shell brown, chestnut-brown or greenish-brown, with both narrow and wide darker-brown spiral lines; unicolored unbanded shells were not rare.

Size of full-grown shells: Very variable, W 27-57 mm; H 30-62 mm.

Distribution: This widely distributed species inhabits a wide variety of waters, both clean and polluted. It is very common in the central and northeastern parts of the country, is rare in the north, and has never been found in the south. The central provinces from which *Pila pesmei* has been frequently collected are Sing Buri, Lop Buri, Angthong, Suphan Buri, Nontha Buri, Chachoeng-sao, Chon Buri, Ratcha Buri and Phetcha Buri. The northeastern provinces

FIG. 8. Shells of *Pila pesmei*. 1,2, Suphan Buri; 3, Phetchabun; 4,5, Chon Buri; 6, Phayao; 7-9, Ubon Ratchathani.

FIG. 9. Distribution of *Pila pesmei.*

Pila polita (Deshayes 1830)
(Fig. 10)

where *P. pesmei* has been found are Loei, Udonthani, Khon-kaen, Kalasin, Roi-et, Yasothon, Ubon Ratchathani, Si-sa-ket, Buri-ram and Nakhon Ratchasima (Fig. 9).

Pila pesmei is found in slow-moving waters (rivers and streams) and in standing waters (pools, ponds, roadside ditches, and even in rice fields). The water may be dirty or clean and its surface water seems always to be partly covered by aquatic plants. *Pila pesmei* is sympatric with *P. ampullacea* and *P. polita*, but the two species are found in different proportions, depending on the season. Populations of *P. pesmei* increase in size from July to September, and the snails are very common in October through December. Specimens are rarely seen during April through June. In their natural habitats, *P. pesmei* can aestivate 1-3 ft underground. In the laboratory, they can aestivate for at least one year.

FIG. 10. Shells of *Pila polita*. 1,2, Bangkok; 3,4, Phayao; 5, Chon Buri.

Pila polita (Deshayes 1830)
(Fig. 10)

Shell large, glossy, moderately thick, oval to subglobosely conic, with a moderately high, conical spire. Shell with 6½ whorls, the body whorl being evenly convex. Aperture oval, retroverting very little laterally. The width of the aperture is about half the aperture height, which is less than ¾ of the shell length. Parietal callus thin and wide; lip sharp, thin but strong, orange or purplish-orange colored. Operculum thin, with steel-blue nacre on the inner surface. Umbilicus very narrow, usually covered over by the inner lip of the mouth. Shell unbanded, brown, chestnut-brown, or greenish-brown.

Size of full-grown shells: W 40-60 mm; H 50-85 mm.

FIG. 11. Distribution of *Pila polita*.

FIG. 12. Shells of the Thai species of *Pila*. *P. ampullacea*: 1, Chon Buri; 2, Bangkok. *P. angelica*: 3, Songkhla. *P. pesmei*: 4, Kalasin; 5, Suphan Buri; 6, Chon Buri. *P. polita*: 7, Bangkok. *P. gracilis*: 8, Songkhla; 9, Pattani.

Distribution: Common in the central, northeastern and northern provinces. Specimens have not been found in Prachuap-khiri-khan or in the south. The central provinces from which *Pila polita* has been most collected are Bangkok, Prachin Buri, Chon Buri, Rayong, Phetcha Buri, Sing Buri, Lop Buri and Nakhon-sawan. The northeastern provinces are Loei, Udonthani, Sakonnakhon, Khon-kaen, Kalasin, Chaiyaphum, Buri-ram, Surin, Si-sa-ket, Nakhon Ratchasima and Ubon Ratchathani. The northern provinces are Chiang-rai, Phayao, Lampang and Tak (Fig. 11).

Pila polita prefers standing water bodies to streams or irrigation canals. Its habitats are pools, ponds, ditches and water reservoirs which are partly covered by aquatic plants. These snails are very common in the dry season, i.e., from March through June. By then most of the snails are adults. They decrease in number during the rainy season. They probably have difficulty competing with *P. ampullacea* and *P. pesmei*. Young *P. polita* are found during the rainy season, whereas the adults come out in the dry and winter seasons.

Pila polita is difficult to rear in the laboratory. This species prefers low water levels (i.e., the water should not cover the snails). Most of the snails die if they are covered with water when the rains start. If the snails that are induced to aestivate continued to live, they seemed to be controlled by an inner biological clock, even in the laboratory.

Fig. 12 shows shells of all the species. The shell sizes are medium to large or very large.

DISCUSSION

The various species of *Pila* are difficult to distinguish morphologically; their shell characters differ only slightly, leading not only to misidentifications, but to confusion as to just what are the valid species in the genus and as to what characters can be used to define the species. Therefore, my approach was to characterize each species first electrophoretically, studying genetic characteristics and diversity of 11 populations taken as representatives of the different conchological types in the genus in Thailand. Then, after I had more reliable information on the biological species occurring in Thailand, I analyzed and reevaluated their shell morphology in light of this new data. The purpose of this paper is to describe accurately and compare the shells of the species of Thai *Pila*.

Pila angelica is more reversely conical than *P. pesmei*, and large specimens of *P. angelica* generally are larger than the adult *P. pesmei*. The shell and apertural lip of *P. angelica* are thin, whereas those of *P. pesmei* are thick. The lip of *P. pesmei* is very strong and retroverted to maintain its operculum securely. The inner side of the operculum of *P. angelica* is colored differently from that of *P. pesmei*; in *P. angelica* it is steel-blue, while in *P. pesmei* it is silvery pinkish-white.

Brandt (1974) included *Pila angelica* as a large form of *P. pesmei*. It is very difficult to separate *P. angelica* from *P. pesmei* if one studies only the shell characteristics. These two species are very closely related, and obviously share a common ancestor. However, they live allopatrically: *P. pesmei* is widely distributed, but does not occur in the south, while *P. angelica* occurs only in the southern provinces.

Due to its large size, *Pila angelica* must live in habitats with high water levels. However, it has the advantage in being able to exploit both standing and running water, which makes this species very common in the south.

Pila pesmei shows much genetic variability in regard to shell characteristics and the male reproductive organ. As a species it is often misidentified. Brandt (1974) called the small form of *P. pesmei* "*P. gracilis*" because of its size, yellowish-orange lip and banding pattern similar to *P. gracilis*. *Pila pesmei* specimens with large shells may be confused with *P. angelica* (see above). The shell size of *P. pesmei* is variable, ranging from medium to large. The unique character of the shell is the thick, retroverted lip with a wide parietal callus. The shell form is also variable; one can find populations with the typically well-rounded globose

shells, and other populations with the slightly reversedly conical form resembling the shape characteristics of *P. angelica*. Not only does the shell form have variability, but in males there is also variation in the position of the duct which runs through the renal vas deferens. Chon Buri and Suphan Buri *P. pesmei* have the duct at the apical part of the renal vas deferens, whereas in *P. pesmei* from Ubon Ratchathani the duct is at the base. The duct of the Kalasin population is at the middle of the globular structure of the renal vas deferens.

As mentioned above, *Pila pesmei* can be misidentified as *P. gracilis* because of the similar appearances of the two species. However, *P. pesmei* has certain characteristics which distinguish it from *P. gracilis*. The shell of *P. pesmei* is more rounded and is thicker than that of *P. gracilis*. The nacre of the operculum of *P. pesmei* is silvery pinkish-white, whereas in *P. gracilis* it is steel-blue. *Pila pesmei* is widely distributed, but does not occur in the south, whereas *P. gracilis* is found only in the southern provinces.

Pila pesmei lives alone in some habitats, but it is often found sympatrically with *P. ampullacea* and *P. polita*. *Pila pesmei* is present in the highest proportion, compared to *P. ampullacea* and *P. polita*, during the middle of the rainy season through the middle of winter. It does not need a very high level of habitat water. So it easily inhabits rice fields and other water bodies which dry up during summer. *Pila pesmei* probably is able to withstand drought for a long time because of its thick shell and operculum.

Pila ampullacea is not difficult to distinguish; it has a uniquely white or purplish-white lip. The shell is generally large to very large, and usually lacks bands. The distribution of *P. ampullacea* is not quite as broad as Brandt (1974) described. He reported that *P. ampullacea* was found in all provinces except Mae Hongson, the northernmost province. Actually, *P. ampullacea* is common only in the central provinces, and does not occur in the south. Brandt probably identified young southern *P. angelica* as a *P. ampullacea*, because immature specimens of *P. angelica* do not develop the yellowish-orange color of the lip.

Pila pesmei and *P. ampullacea* are very closely related. They share the same color of nacre of the operculum (silvery pinkish-white), and they have a similar shell shape, which is well-rounded globose. *Pila ampullacea* has a slightly thinner shell than *P. pesmei*. Because of their moderately thick shells with thick opercula, both *P. ampullacea* and *P. pesmei* can aestivate for long periods of time.

Pila ampullacea is usually found sympatrically with *P. polita*. In some areas, such as in Chon Buri, *P. ampullacea* is found in unequal amounts with *P. pesmei* and *P. polita*. *Pila ampullacea* is very common from the beginning through the middle of the rainy season, during which time the water level of the habitat is high. *Pila ampullacea* needs high water levels. *Pila ampullacea* decreases in number during the end of the rainy season (October-November), a time during which *P. pesmei* is increasing in number. During the winter and summer seasons, before the rain starts, *P. ampullacea* burrows into the ground and aestivates to avoid the drought. Only rarely is *P. ampullacea* found in a water body during the dry season.

Pila polita has a unique, easily recognizable shell shape. It also has a very glossy shell texture. *Pila polita* must have diverged from the same common ancestor as *P. gracilis*; apparently, the two species are closely related. *Pila polita* and *P. gracilis* both have an oval or ovate-conical shell shape and a thin operculum with steel-blue nacre.

In pools and ponds in which the water does not dry up during the dry season, *Pila polita* is found in great numbers from March through June, during which time *P. ampullacea* and *P. pesmei* are scarce. If there are *P. ampullacea*, *P. pesmei* and *P. polita* living sympatrically in a habitat, *P. polita* increases in number last. That is, *P. ampullacea* is most abundant first, then *P. pesmei* increases in number while *P. ampullacea* decreases, and finally *P. polita* becomes the major group during summer. It is an advantage for *P. polita* to exploit a water body without any competitors. Probably *P. polita* is not able to compete with *P. ampullacea* and *P. pesmei*. It, therefore, has unusual behavior, by which it goes underground and remains dormant, tightly closing its operculum during the short rainy season.

The opercular characters of *P. polita* are very similar to those of *P. angelica* and *P. gracilis*. The operculum is thin, nacreous, and steel-blue in color. *Pila angelica* and *P. gracilis* do not aestivate very long, probably because the ground in the south is generally or often moist. *Pila polita* may have the ability to remain in the wet ground for a period of three to four months, as do *P. angelica* and *P. gracilis*. Its very shiny shell may help repel water, and its thin operculum does not seem to aid in keeping water within the shell.

ACKNOWLEDGEMENTS

I wish to thank J.B. Burch, Peter G. Meier, Claire L. Schelske, Eugene F. Stoermer and E.S. Upatham for their advice and support, Raat Channavat for assistance in field work and for helpful discussions on various aspects of the biology of *Pila*, and Sanay Keawjam, Visut Tulsuk, Pisinee Lee and Kittisak Trisilpa for help in collecting.

Grateful acknowledgement is made to the World Health Organization for a Research Training Grant and to the Museum of Zoology, The University of Michigan, for Hinsdale Scholarships.

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Malacological Review, 1986, 19: 83-89

POPULATION RESPONSES OF THE SNAIL *BULINUS (PHYSOPSIS) ABYSSINICUS* TO DIFFERING INITIAL SOCIAL AND CROWDING CONDITIONS[1]

M.D. Ahmed, E.S. Upatham, W.Y. Brockelman and V. Viyanant

ABSTRACT

A study of growth, reproduction and survival of the snail *Bulinus (Physopsis) abyssinicus*, the intermediate host of *Schistosoma haematobium* in the Somali Democratic Republic, was carried out in the laboratory. The purpose of this study was to determine the effects of isolation and crowding on life history characteristics and the intrinsic rate of natural increase in the presence of ample food supply. The three treatments used included snails kept in isolation, and snails kept at initial densities of four and eight per container with 640 ml of water.

The isolated snails attained the largest size (average shell length 11.0 mm), the highest survival rate (90%) and had the lowest reproductive rate (28 eggs per snail). Their intrinsic rate of natural increase was 0.077/day. Both high and low initial density groups showed somewhat slower growth, lower survivorship and higher egg production than snails in isolation. Their intrinsic rates were both about 0.10/day, but snails in the high initial density group had a lower survivorship and slightly higher growth rate and egg production than those in the low initial density group. Individual reproduction was thus inversely related to survivorship. For snail culture purposes, the lower initial density is most favorable.

INTRODUCTION

Bulinus (Physopsis) abyssinicus (Martens) is the only intermediate host of *Schistosoma haematobium* (Bilharz) in the Somali Democratic Republic (Baruffa, 1962; Koura et al., 1981), where it occurs along the two permanent rivers, the Juba and the Shebele. An understanding of the epidemiology of schistosomiasis in the irrigated areas along these rivers is of great significance because these areas contain the only arable lands in the country.

The snail occurs in a variety of seasonal and permanent habitats and will be difficult to control (Upatham et al., 1981). It has been found 200 km south of the Juba River, transported by seasonal flooding or perhaps by animals or in water jars carried by nomads (Koura et al., 1981). *Bulinus (P.) abyssinicus* can aestivate in dry river beds (Cahill, 1971). Such a snail must have the ability to increase in numbers rapidly at periodic intervals.

The study of the innate capacity for increase (Andrewartha & Birch, 1955) of a snail vector is useful in order to establish the rate at which it can recover from low population levels, and to establish optimal conditions for laboratory management and experimentation. Laboratory experiments were undertaken to determine the effects of isolation and varying initial density on growth, survival, age-specific fecundity and the intrinsic rate of increase of *Bulinus (P.) abyssinicus*.

MATERIALS AND METHODS

Culture conditions

A colony of *Bulinus (Physopsis) abyssinicus*, established from field-collected snails from Somalia, has been maintained at the Center for Applied Malacology and Entomology, Faculty of Science, Mahidol University, since 1979. Snails have been kept in conditioned tap water and fed boiled lettuce. Offspring

[1] This investigation was supported by the United Nations Development Programme/World Bank/World Health Organization Special Programme for Research and Training in Tropical Diseases.

hatched from eggs laid by these snails over a 24-hr period were used in the experiments. Most eggs hatched after 5-6 days.

Newborn snails were fed a suspension of the blue-green alga *Nostoc muscorum*. Young snails were transferred several times to new aquaria to eliminate the annelid *Chaetogaster*, a frequent pest in our snail cultures. Fresh, boiled and dried lettuce were added to their diets after two weeks. Culture water was changed and the snails were fed every day during the experiment. All snails received aeration, and they were raised at normal room lighting and temperature (25-27°C). Small pieces of chalk were added to the containers weekly.

Snails were measured at the start of the experiment at the age of seven days, as well as once a week during the experiment, over a 1-mm grid under a stereo-dissecting microscope. Eggs laid were removed and counted every day.

The experimental snails were raised in 75 rectangular transparent plastic containers, 9.0 x 20.5 x 5.0 cm, each with four compartments holding 160 ml of water per compartment. In some containers, the inner partitions were removed (see treatments below).

Experimental design and analysis

A cohort of 400 snails was randomly assigned to three treatments, each using 25 containers. In the first treatment, 100 snails were kept in isolation in 160 ml of water, one per compartment. In the second treatment (low density), 100 snails were placed four per container with partitions removed, or at a density of four per 640 ml. In the third treatment (high density), 200 snails were placed eight per container with partitions removed, or eight per 640 ml. Thus, the initial density of four per container had the same density as the isolated snails, one per 160 ml.

These three treatments were intended to analyze the effects of exposure to other snails and of initial density on growth, fecundity, survival, generation time and the rate of natural increase. The initial densities of four and eight snails were not maintained; densities were allowed to decline during the experiment as mortality occurred, as they would under natural conditions. The differences in egg production and growth among treatments were tested with Kruskal-Wallis one-way analysis of variance.

The net reproductive rate (R_0) was determined by summation of $l_x m_x$ data over weeks. Then the mean generation time (T), defined as the mean period elapsing between the birth of parents and the birth of offspring, was estimated approximately as:

$$\hat{T} = \frac{\Sigma x l_x m_x}{\Sigma l_x m_x}$$

The capacity of increase was determined from the Lotka equation:

$$\Sigma e^{-rx} l_x m_x = 1$$

by substituting several trial values of r, and plotting them against $\log \Sigma e^{-rx} l_x m_x$ (DeWitt, 1954). A straight line is obtained which allows a better approximation of r where the line crosses zero. The approximation was made to three significant figures. The first trial value was obtained from the approximation

$$r_1 = \frac{\ln R_0}{\hat{T}}$$

Finally, the generation time was determined more precisely from

$$T = \frac{\ln R_0}{r}$$

RESULTS

Survivorship

Crowding imposed a thinning effect on the populations of the snails (Fig. 1), which was greatest at high initial density. At the end of the experiment (week 14), 40.0% of the snails survived at high initial density, 65% at low initial density, but 90.0% of those kept in isolation survived.

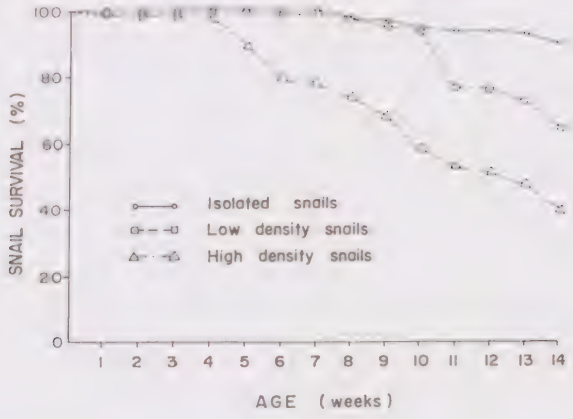

FIG. 1. Survivorship of *Bulinus (Physopsis) abyssinicus* in the three treatments.

Egg production

Egg laying began in all groups of snails during the sixth week of the experiment, at a mean size of 5 mm (Figs. 2 and 3). Snails kept in groups started reproducing at a smaller size than those kept in isolation. The isolated snails reached their maximal fecundity at a size of 11-12 mm, whereas snails in the groups reproduced maximally at around 9.5-11.0 mm. The snails in the low and high initial density groups followed a similar fecundity-size pattern (Fig. 2), as their effective densities converged. Fecundity of isolated snails, however, was much lower at corresponding body sizes. The isolated snails produced an average of 258 eggs per snail, while the snails in groups averaged about 730 eggs per snail. These differences were significant ($p < 0.01$).

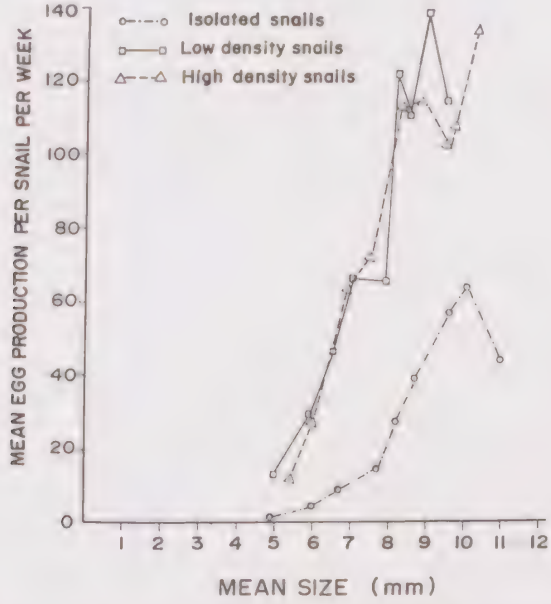

FIG. 2. Relationship between number of eggs produced per week and mean shell length for each treatment. FIG. 3. Egg production in *Bulinus (Physopsis) abyssinicus* in relation to age in each treatment.

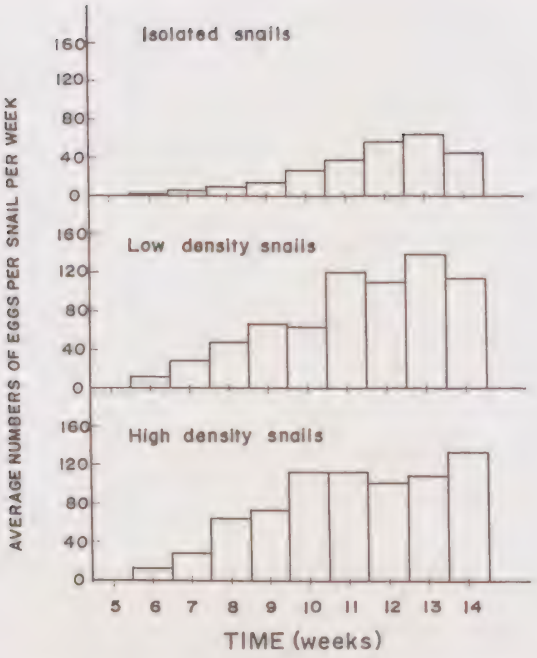

FIG. 3. Egg production in *Bulinus (Ph.) abyssinicus* in relation to age in each treatment.

Growth

The mean sizes of the snails in the different treatments diverged during the experiment. The snails in isolation attained the largest mean size, 11.0 mm, while the snails in the 8-snail groups attained 10.3 mm, and those in the 4-snail groups attained an average of 9.5 mm. The mean lengths were highly significantly different among treatments ($p < 0.001$; one-way analysis of variance).

Snails in the high initial density treatment grew slightly faster than those at low initial density during weeks 8 to 11. The snails at high density gained 0.70 mm during this period, while those at low density gained 0.51 mm. However, each container in the high density treatment had lost 2-4 snails and the average density was 4.5 snails at 11 weeks, compared with 3.5 snails in the lower density treatment. Thus, differences in density were nearly erased.

The coefficient of variation was similar among the three treatments: 48.6% (isolated snails), 45.6% (low density) and 47.5% (high density), respectively.

Intrinsic rate of natural increase

The intrinsic rate of natural increase of the isolated snails was 0.077/day, whereas for the other treatments it was approximately 0.10/day (Table 1). Snails in isolation either reproduced later or not at all during the whole period.

Snails in the initial 8-snail groups produced more eggs and had a slightly shorter mean generation time than those in the 4-snail groups, which compensated for their reduced survivorship. The lower density treatment had a net reproductive rate 44% higher than that of the higher density treatment.

Within the 8-snail treatment, the value of r in those containers with more than four snails at the end of the experiment was similar to that in containers with four or fewer snails (Table 2). Again, the higher reproduction in the less crowded containers (< 4 snails) at the end of the experiment and the shorter generation time compensated for lower survivorship.

TABLE 1. Summary of statistics of all treatments on *Bulinus (Physopsis) abyssinicus*.

Statistic	Isolated snails	Low initial density	High initial density
Intrinsic rate of natural increase (r)	0.077/day	0.101/day	0.100/day
Net reproductive rate (R_0)	243.7	623.4	433.9
Egg production/snail/week (weeks 6-14)	28	78	83
Mean generation time (T) (days)	71.4	63.7	60.7
Mean size, 5th week (mm)	4.1	4.3	4.4
Mean size, 14th week (mm)	11.0	9.5	10.3
Survivorship to week 14 (%)	90	65	40

TABLE 2. Comparison of statistics for high density containers (>4 snails) and low density containers ($\leqslant 4$ snails) within the high initial density treatment on *Bulinus (Physopsis) abyssinicus*.

Statistic	Containers with more than four snails	Containers with four or fewer snails
Intrinsic rate of natural increase (r)	0.100/day	0.100/day
Net reproductive rate (R_0)	352	538
Egg production/snail/week (weeks 6-14)	86	78
Mean generation time (T) (days)	58.6	62.9
Mean size, 5th week (mm)	4.4	4.3
Mean size, 14th week (mm)	10.3	10.1
Survivorship to week 14 (%)	25	72

DISCUSSION

Initial density differences (four and eight snails per container) were not maintained throughout our experiment; mortality was allowed to change effective densities. Although this did not permit an examination of continuing individual responses to the densities, it did allow a more realistic examination of population responses to given initial conditions.

The most interesting result was the apparent regulation of overall population response — as measured by the intrinsic rate of increase — at different densities. Mortality compensated for differing initial densities, and although mean rates of egg laying, growth rates and survivorship differed between containers at different densities, all had nearly the same r . This phenomenon is the result of individual snails having the ability to compensate for environ-

mental stresses to maximize individual reproductive success. Only the isolation treatment (which was not a "density" treatment) resulted in drastically reduced reproductive success.

These results are somewhat surprising, because if population density is regulated we should expect r to be inversely related to density. By achieving a shorter generation time, the high density was able to "postpone" effects of crowding to future generations. If snails vary individually in their density responses, perhaps having a higher initial number permits greater selection for individuals that reproduce better under crowded conditions.

Although these snails are hermaphroditic, male and female organs might not mature at the same time, and cross-fertilization may be essential for normal reproduction in any event.

Mortality in animals is frequently found to be inversely related to reproduction. Murdoch (1966) observed a higher mortality rate among flightless beetles, *Agonum fuliginosum*, in females housed with males than in females kept alone. Reproduction uses energy at the expense of body maintenance and growth. Ritchie et al. (1962) noted low reproduction and good survival in *Australorbis* (= *Biomphalaria*) *glabratus* (Say) when they were reared together. Shiff (1964a) found that *Bulinus (Physopsis) globosus* (Morelet) grew faster when raised singly. Our results show that singly-reared snails survived and grew better than those reared in groups. These snails used more energy for growth and survival and less for reproduction.

The early outburst of egg laying observed among snails raised in groups, followed by a high mortality (especially among high initial density snails), is generally consistent with the generalization of Stearns (1976) that high reproductive effort early in life for an iteroparous species is usually associated with a cost to parents in terms of reduced survival. Minchella & LoVerde (1981), exposing *Biomphalaria glabrata* with miracidia, noticed a burst of egg production among parasitized snails followed by cessation of snail reproduction and higher mortality.

One problem with this interpretation, however, is that mortality began increasing in the 8-snail groups just prior to first reproduction. In the 4-snail groups, mortality began increasing at around week 11, well after the onset of egg laying (Figs. 1 and 2). These differences are more easily attributed to a water-borne inhibiting factor (Levy et al., 1973; Thomas et al., 1975) than to a direct effect of reproduction on survival. Thus, although the experiment has not provided any direct evidence for water-borne inhibitors affecting growth, the differences in survivorship between low and high initial densities are difficult to explain completely otherwise, as food was not limiting. The isolated snails and the 4-snail groups began at the same density, but the isolated snails suffered little mortality. Differences in egg production between low and high density containers within the high density treatment also suggest inhibition of some sort.

Bulinus (Physopsis) abyssinicus thrive when they are raised in as little as 160 ml of water per snail with aeration, but even at this density crowding was probably responsible for some mortality. A laboratory density of no more than one snail per 300-500 ml is therefore recommended. The mortality is evidently not due to food shortage but to some other undetermined density effect. Although they are hermaphroditic, optimal reproduction occurs only when they are maintained in groups.

A rate of increase of 0.101/day is relatively high for a pulmonate snail. Comparable values for schistosome vectors include 0.047 for *Bulinus (Physopsis) globosus* (Rhodesian origin) (Shiff, 1964b); 0.030-0.034 for *Biomphalaria pfeifferi* (Krauss) (Rhodesian origin) (Shiff & Husting, 1966; Shiff & Garnett, 1967); 0.061 for *Bi. pfeifferi* (Tanganyikan origin) (Sturrock, 1966); and 0.063/day for *Bi. glabrata* (St. Lucian origin) (Sturrock & Sturrock, 1972). *Bulinus (P.) abyssinicus* can double its population in seven days. Dazo et al. (1966) calculated that in optimum field conditions *Bu. truncatus* (Audouin) and *Bi. alexandrina* (Ehrenberg) can double their numbers in 14-16 days.

The capacity for increase and population responses to crowding in *Bulinus (Physopsis) abyssinicus* suggest a snail with high dispersal ability adapted to highly unstable environments.

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Malacological Review, 1986, 19: 91-98

PATTERNS OF CORROSION AND ABRASION INDUCED BY MEDITERRANEAN LAND SNAILS ON LIMESTONE ROCKS

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ABSTRACT

Some land snails in the Mediterranean area regularly dissolve calcium carbonate in fissures of limestone rocks with the skin of the soles of their feet. Typical weathering patterns are formed in hard limestone rocks as a result of snail and slug abrasion of the lichenized rock faces. The typical weathering patterns of honeycombs or small caves with perforated roofs can be used for studies on the climate of the past.

INTRODUCTION

The role of gastropods in the weathering of limestone rocks has been studied from various points of view. Kühnelt (1933) studied the dissolution of limestone by *Helix aspersa* Müller near Gijon, Spain, and by *H. mazzuli* Jan near Palermo, Sicily, which form typical holes in the rock. Avnimelech (1939) attributed the formation of some components of the karstic topography near Jerusalem to land snail activity. A few species of the genera *Levantina, Helix, Buliminus, Chondrulus* and *Leucochroa* that he named "the *Levantina hierosolyma* Boiss. community" were involved. He suggested the rate of total rock weathering by snails to be 0.002 mm/year. Schneider (1976), Torunski (1979) and Schneider & Torunski (1983) studied the biogenous weathering of limestone coasts on the Adriatic Sea; they termed "corrosion" the dissolution of limestone by endolithic fungi, algae, cyanobacteriae and lichens. The mechanical removal of limestone by gastropods (e.g., *Littorina neritoides* Linnaeus, *Monodonta turbinata* Born and *Patella coerulea* Linnaeus) and echinoids (*Paracentrotus lividus* Lamarck) was regarded by these authors as "abrasion".

Schmid (1929) studied the abrasion of limestone by the land snails *Chondrina avenacea* Bruguière and *Pyramidula rupestris* Draparnaud in Germany and in the Alps. He concluded that they consume mainly the fungal component of the endolithic lichens and excreted algae and limestone particles. Danin & Garty (1983) studied the patterns of weathering on desert stones in the Negev, Israel. These stones displayed micro-grooves that were the result of two species of *Euchondrus* feeding on the fungal component of endolithic lichens.

The present article deals with the weathering patterns induced on limestone in the Mediterranean mountainous part of Israel by two genera of land snails, *Levantina* and *Buliminus*. These land snails presumably dissolve calcium carbonate for the purpose of building their shells and abrade the rock surface while feeding on endolithic lichens.

LOCATIONS AND ENVIRONMENT

The principal areas of field observations are presented in Fig. 1. The mean annual rainfall of the sites in Jerusalem, Mt. Gilboa and Mt. Carmel is above 400 mm; that of Ein el Fawwar is 200 mm, and that of Mt. Rahama and Mt. Romem is 100 mm (Rosenan, 1970). The rocks that are populated by snails become wet only in the winter, mostly because of rain; dew causes wetting of these rocks only rarely (Danin & Garty, 1983, and unpubl. data). The activity of the land snails studied here could be detected mainly on rock outcrops exceeding 1 m in length and containing deep fissures and crevices. The studied rocks were hard massive limestones of the Cretaceous and the Eocene eras.

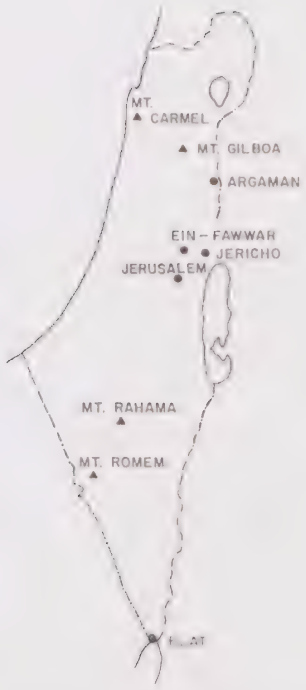

FIG. 1. Location map of Israel.

MATERIALS AND METHODS

The land snails studied here were *Levantina caesareana* Parreyss, *L. hierosolyma* Boissier and *Buliminus labrosus* Olivier. One species of slug, *Deroceras reticulatum* Müller, also was observed grazing on lichenized rock faces.

Patterns of weathering induced by snails were observed in the field. Living *Levantina caesareana* and pieces of rocks from their original habitat were collected in winter 1982 from Mt. Gilboa. Their grazing habits were studied by placement in a plastic box of a few snails on a piece of rock, populated mainly by the endolithic lichen *Caloplaca alociza* (Massalonge) Migula. The rock was wetted and the box was sealed with glass. After one night, radula marks were sought on the rock with the aid of a dissecting microscope.

A few *Levantina caesareana* were put in a sealed dry plastic box with flat polished limestone for a month in winter 1982.

Snail specimens are deposited in the Department of Zoology, and lichens in the Department of Botany, The Hebrew University, Jerusalem.

RESULTS

Honeycomb pattern

The prominent pattern of weathering that was attributed to snails looks like a honeycomb (Kühnelt, 1933) (Fig. 2) or a small cave with 2-3 cm holes in its roof (Fig. 3). This pattern was observed, with snails inside the holes, in Jerusalem, Mt. Carmel, Mt. Gilboa and near Argaman (Fig. 1). *Levantina caesareana* specimens were found at the deep ends of the cylindrical holes in the rocks. The walls of the holes were always smooth. A few stages in the development of these patterns were observed in the field. Snails were hiding in fissures that were slightly wider than the height of their shells. In winter, the soles of their feet touched the rock, whereas in summer, when the snails aestivate, their feet were not in direct contact

FIG. 2. A honeycomb weathering pattern created by *Levantina caesareana* on fissure of a limestone cliff.

with the rock. The snails were seen in groups of dozens in such fissures. The walls of these fissures were rough or had smooth depressions, 2-3 cm in diameter. There were fissures with 2-3 cm deep circular holes (Fig. 2); others were much deeper and formed small cave-like depressions above the fissure up to 15-20 cm from the lower wall of the fissure (Fig. 3). Stones or boulders that had been dislodged from the main rock outcrop also displayed the honeycomb pattern of weathering.

The diameter of holes in the "honeycombs" or "caves" was 2-3 cm in Mt. Carmel, Mt. Gilboa and Jerusalem. Here, the mean weight of *Levantina caesareana* was 4.1 ± 1.3 g (Heller, pers. comm.). In Argaman, under drier climatic conditions, the diameter of holes was 1-1.5 cm, and *L. caesareana* shells weighed only 1.9 ± 0.58 g (Heller, pers. comm.).

Specimens of *Levantina caesareana*, *L. hierosolyma* and *Buliminus labrosus* occurred in fissures and rock crevices of desert areas at Ein el Fawwar, Mt. Rahama and Mt. Romem. However, no active formation of "caves" and "honeycombs" was observed there. "Honeycombs" that were made in the past were found on cliffs and boulders at Ein el Fawwar. The size of the holes composing the honeycombs was similar to that of those at Mt. Carmel or Mt. Gilboa. Similar relic structures were observed in August 1983 in Crete, at the southern mouth of the Samaria Gorge.

In order to study rock dissolution by the skin of the sole of the foot, *Levantina caesareana* snails from Mt. Gilboa were kept in a sealed box with polished limestone. The polished faces (white in Fig. 4) became dull in a heart-shaped spot where the foot sole was attached for a month. The limestone surface lacked radula marks and was similar to the surface of the hole walls.

Jigsaw puzzle-like pattern

Levantina caesareana snails that were allowed to graze on a lichenized piece of rock from Mt. Gilboa, with mainly *Caloplaca alociza*, preferred to graze along the meeting zones of thalli. The lichen *C. alociza* penetrates to a depth of 1-2 mm into the rock. Most of the

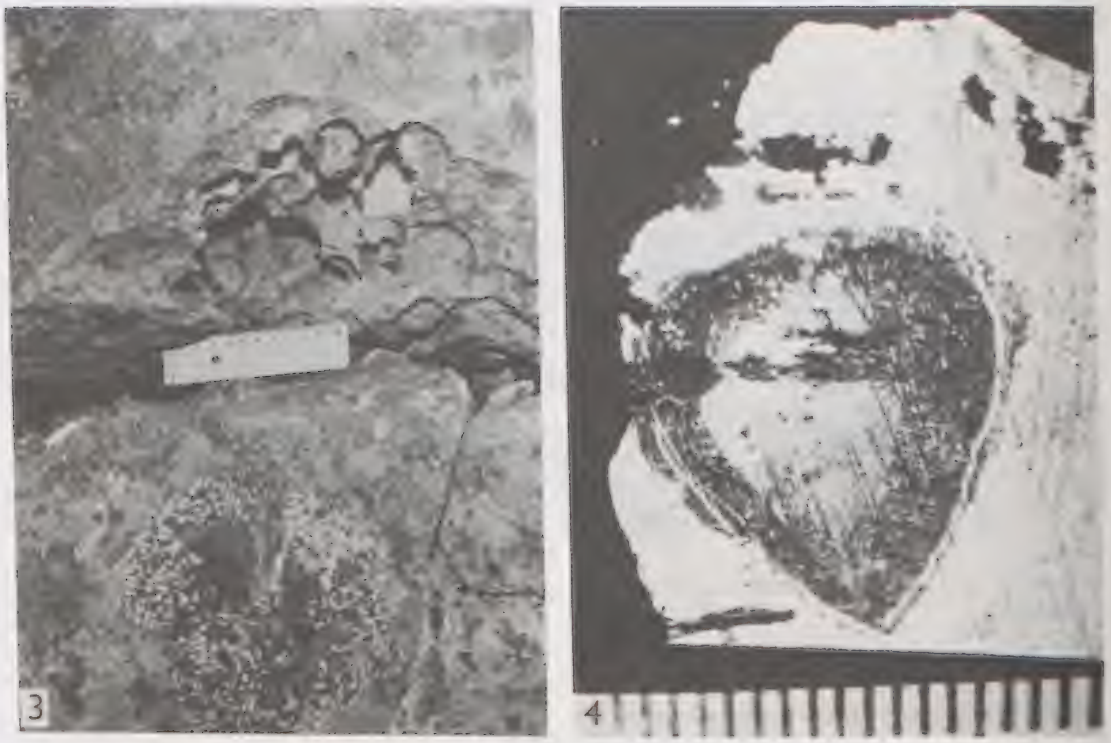

FIG. 3. A small cave caused by dissolution of linestone near a fissure where land snails hide. Note the "labyrinth" weathering pattern of the oval thallus of an endolithic lichen below the 10 cm scale. FIG. 4. A heart-shaped dissolution pattern on polished limestone created by the foot of *Levantina caesareana* after one month.

radula marks that were observed on the rock were in the micro-grooves at the meeting zones of thalli (cf. Danin & Garty, 1983). Most of the micro-grooves shown in Fig. 5 seem to be a result of snails' grazing on the fungal component of the endolithic lichen community (Fig. 6). The micro-grooves were 2-3 mm wide and deep. There were a few rounded depressions that were also a result of snails' grazing.

The same lichen communities, when they developed on rocks without crevices and depressions or far from such rocks, had the "jigsaw" pattern, but with narrow and shallow micro-grooves like those at the center of Fig. 5.

Labyrinth pattern

The pattern seen below the fissure in Figs. 3 and 7 is a result of prolonged gastropod grazing on the endolithic lichen *Verrucaria* sp. The slug *Deroceras reticulatum* was observed grazing on such a lichen on Mt. Gilboa during a rainy day. The slug was brought to the laboratory and was allowed to graze on a fresh lichenized rock placed in a plastic box. The slug's radula marks were observed in the winding shallow grooves. This endolithic *Verrucaria* sp. differs from *Caloplaca alociza* in that it corrodes the rock to a depth of 10 mm, thus

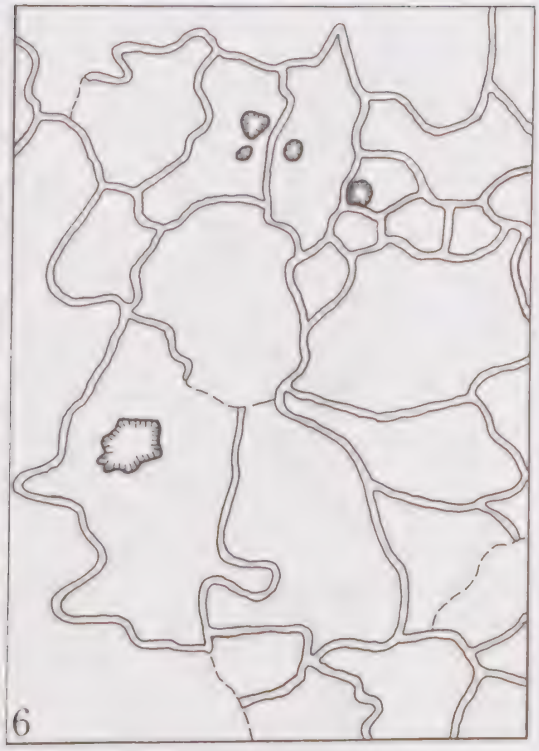

FIG. 5. A jigsaw puzzle-like pattern on hard limestone. After facing the soil for a long time, the micro-grooves created by the lichens and extended by the snails are prominent. See further details in Fig. 6. FIG. 6. A sketch of the weathering patterns displayed in Fig. 5: – – – micro-grooves created by the activity of the fungal component of the lichen thalli; ═══ micro-grooves extended by the grazing activity of snails; a crater-shaped depression resulting from the grazing of snails at the center of lichen thallus.

making the rock surface softer. The thalli of *Verrucaria* sp. with the "labyrinth" pattern are much larger than those of *C. alociza*, and there are no prominent micro-grooves in meeting zones of thalli. The labyrinth pattern is rather variable; some grazed thalli look like concentric circles. Most of the lichen's peritheeia are missing from the grazed paths. This may indicate a preference for grazing on the fungal part of the lichen, as reported by Schmid (1929).

DISCUSSION

It is assumed that the honeycomb weathering pattern is formed in limestone rocks only under Mediterranean conditions. The use of the skin of the sole of the foot to obtain calcium carbonate was demonstrated by Kühnelt (1933), by Fournie & Chetail (1983), and in the present study (Fig. 4). In Jamaica, only up to 33% of the carbonate used by land snails to build their shells is derived from rocks (Goodfriend & Hood, 1983). It is not known how much of the carbonate in the shell of the Mediterranean land snails is derived from rocks.

Calculating the rate of hole formation may help in reconstructing the time-span over which Mediterranean conditions prevailed in an area under review. A common hole in a honeycomb pattern related to *Levantina caesareana* may be 3 cm in diameter and 5 cm deep. Volume

FIG. 7. A labyrinth pattern of weathering created by the grazing of an endolithic lichen by gastropods.

of the hole = 1.5 x 3.14 x 5 = 23.56 cm^3. Weight of calcium carbonate removed = 23.56 x 2.71 g/cm^3 = 63.85 g. The specific weight of calcite is 2.71 g/cm^3. The mean weight of a shell from the Mediterranean populations of this snail is 4 g (Heller, pers. comm). It takes approximately five years for this snail species to achieve its maximal shell weight (Heller, pers. comm). If all the calcite for building the shell is derived from dissolution of the rock, then the dissolution of the hole may take: T = 63.85 g / 4 g x 5 y = 79.8 y. If the figures presented by Goodfriend & Hood (1983) are correct also for the Mediterranean land snails, it can be assumed that it will take some 240 years to form a single hole 3 x 5 cm. Further

calculations require better knowledge of the population densities and dissolution habits of the various snail species.

The honeycomb weathering pattern already was known from the western Mediterranean (Kühnelt, 1933) and is reported now from the eastern Mediterranean. There are sharp boundaries between the Mediterranean zone and the semi-arid and desert zone in Israel (Danin, 1983). This situation enables us to determine the extent of the honeycomb weathering pattern. Finding a fossil weathering pattern of honeycomb provides evidence of prevalence of Mediterranean climate in the past at the site under study. Fossil honeycomb patterns were found in a 2,000-year-old Hasmonean site near the Jaffa Gate and in the 2,700-year-old Broad Hezkiah Wall (Danin, 1985). It is suggested that the climate 2,000-2,700 years ago was similar to that of the present time. Fossil honeycomb patterns found near Ein el Fawwar suggest that the climate there was wetter in the past. This conclusion is supported by fossil weathering patterns of other organisms indicating a wetter climate in the Judean Desert in the past (Danin et al., 1982). There are indications that the wet period might have been in the Neolithic Period (Danin, 1985).

In his recent review of literature concerning the consumption of lichens by gastropods, Lawrey (1984) did not mention the grazing of endolithic lichens by gastropods. Although that kind of grazing has been known since the pioneer study of Schmid (1929), not much was reported on the weathering patterns appearing in such lichen-gastropod ecosystems. One may ask why gastropods would graze on endolithic lichens. The snails and slugs studied here feed mostly on dead organic material (Heller, pers. comm.) which is present in relatively unlimited quantities where they live. It is suggested here that the constant consumption of lichens by gastropods may be a result of the latter's need for essential elements that are concentrated in lichens. Experimental study (Lawrey, 1983) has proved that epilithic lichens with high concentrations of essential elements (i.e., P, K, Mg, Mn, Fe, B, Cu and Zn) were most likely to produce defense compounds. The paucity of defense compounds in endolithic lichens already has been reported by Schmid (1929). Chemical analyses of endolithic lichens in Israel revealed high content of essential elements and absence of lichenic acids (Kushnir, 1979).

The gastropods graze on soft parts of the rock, including the fungal component of the endolithic lichens (Schmid, 1929). As a result, two kinds of weathering patterns develop. *Verrucaria* sp. corrodes the hard limestone to an extent that enables slugs and probably other gastropods to abrade the lichen-rock surface. The result is a labyrinth pattern of broad and shallow winding grooves where the slugs prefer to pass and graze. *Caloplaca alociza* thalli do not cause such softening of the rock; the snails prefer to consume the fungal component of the thallus, thus making the micro-grooves at the meeting zones of lichen thalli deeper and wider (Danin & Garty, 1983). As a result, a prominent network of micro-grooves forming a jigsaw puzzle-like pattern is formed on the rock faces. These two weathering patterns are typically Mediterranean and may be used in palaeoclimatic investigations.

ACKNOWLEDGEMENTS

This study was supported by the Fund for Basic Research administered by the Israel Academy of Science and Humanities. I thank J. Heller, Department of Zoology, The Hebrew University of Jerusalem, for identifying the gastropods and providing data for this study. I thank Anne B. Thistle, J. Heller and W.H. Heard for the critical reading of the manuscript.

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Malacological Review, 1986, 19: 99-104

ECOLOGY OF SOME FRESHWATER PULMONATES FROM CUBA

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ABSTRACT

Fluctuations in the density of five species of Cuban freshwater pulmonate snails were studied in natural conditions during a 16-month period. Growth curves calculated by the von Bertalanffy equation show that *Planorbella duryi* may not be as successful a competitor of pulmonates as expected, at least in seasonal ponds. Abiotic factors did not exert great influence in the variation of densities during the time of study.

INTRODUCTION

Little is known about the ecology and other aspects of the biology of Cuban freshwater pulmonate snails, which is unfortunate from the viewpoint of human welfare, because many freshwater snails are intermediate hosts of parasites afflicting both man and domestic animals.

Several Cuban freshwater snails are of medical or veterinary importance. *Biomphalaria havanensis* (Pfeiffer) and *B. helophila* (Orbigny) have been experimentally infected with *Schistosoma mansoni* (Sambon) and are considered to be potential intermediate hosts of schistosomiasis (Richards, 1963; Michelson, 1976). Three species of *Drepanotrema* (*D. anatinum* (Orbigny), *D. cimex* (Moricand) and *D. lucidum* (Pfeiffer)) carry avian trematode cercariae which produce cercarial dermatitis in humans. *Fossaria cubensis* (Pfeiffer) and *Pseudosuccinea columella* (Say) are both intermediate hosts of *Fasciola hepatica* (Linnaeus), which infects both cattle and humans. Under laboratory conditions, *Planorbella duryi* (Wetherby) has been reported to compete with planorbid snail hosts for food and to have a superior reproduction rate and low mortality (Frandsen & Christensen, 1977; Frandsen & Madsen, 1979). Preliminary observations have also pointed to *Physella cubensis* (Pfeiffer) as a competitor of other pulmonate snails, thus also being of potential snail-control value.

This study deals with growth and density in natural habitats of several snails of medical importance, members of the families Planorbidae, Physidae and Lymnaeidae. Voucher specimens have been deposited in the Instituto de Zoologia, Academia de Ciencias de Cuba, and in the Museum of Zoology, The University of Michigan, Ann Arbor, Michigan, U.S.A.

HABITAT, MATERIALS AND METHODS

The studies were carried out under natural conditions between September 1983 and April 1985. Snails for growth studies were kept in breeding cages (Yong & Perera, 1983), which are transparent plastic boxes 40 cm high, 25 cm wide and 25 cm long, with two side windows and one top window made of No. 39 phytoplankton net. The box, provided with floats at the top, was closed and secured to the bottom of the stream or pond by a rope so it could float in a narrow environment. Enough food was given to the snails; light and water exchange were guaranteed by the design of the box. The growth curves were calculated by means of the von Bertalanffy equation, $L_t = L_{oo}\ (1\text{-}e^{-kt})$ (von Bertalanffy, 1938), in which L_t is the shell length at a time t after birth, L_{oo} is the shell length for a zero growth rate, k is a characteristic growth constant and t the age of the animal. The time interval between each measure, a fortnight, was the same. The growth parameters k and L_{oo} were calculated by Walford's method (Walford, 1946).

Planorbella duryi was studied during February 1984 in Treasure Lake (Fig. 1A), which is one of the largest natural lakes in Cuba. The water temperature ranged between 24 and 28°C; the pH was 6. The lake's vegetation includes *Nuphar advena* (Aiton) Aiton f., *Typha dominguensis* (Persoon) and *Eleocharis interstincta* (Vahl) Roemer and Schultes, among others. One hundred nineteen studies were separated

FIG. 1. Four of the habitats studied. a, Treasure Lake; b, Camaguira; c, Batabano; d, Campo Florido.

into eight classes of size (10, 9, 8, 7, 6, 5, 4 and 3 mm) and measured with a calliper (0.05 mm error) with a fortnight interval of time. The measure taken was the maximum diameter considered as the perpendicular between two parallel lines tangent to the outer lip and its opposite side, respectively.

Camaguira pond (Fig. 1B) was used in March 1984 for growth and density studies of *Biomphalaria havanensis* and *B. helophila*. This is a small natural pond with abundant aquatic vegetation and an organic bottom layer. Water temperature was 24-26°C and the pH 6. Eighty-nine *B. havanensis* and 137 *B. helophila* were separated into five size classes (2-3, 4-5, 6-7, 8-9 and 10 mm, and 0.5, 1, 1.5, 2 and 2.5 mm, respectively. The measure considered was the maximum diameter as described in *P. duryi*.

Watercress beds in Batabano (Fig. 1C) were used for growth studies of *Fossaria cubensis* and *Pseudosuccinea columella* during April 1985. These are square areas of 24 x 7 m surrounded by canals that keep the water flowing. The water temperature ranged from 27 to 30°C and the pH was 7.5. Ninety *F. cubensis* and 110 *P. columella* were separated into five size classes (6, 5, 4, 3 and 2 mm). The measure considered was the maximum shell length taken as the length of a perpendicular between two parallel lines and tangent to the apex and the posterior end of the outer lip.

Baseline density studies have been carried out during a 16-month period (September 1983 - December 1984) in order to determine fluctuations of snails during different times of the year (dry and rainy season). Three ponds were used in the study: Camaguira, Mosquito and Campo Florido (Fig. 1D). The latter two have similar vegetation: *Typha dominguensis* and *Hymenachne amplexicaulis* (Rudge) Nees, but Campo Florido is shallower and has also *Bacopa monieri* (Linnaeus) Pennell among aquatic plants.

The snails were sampled every fortnight in a unit of time (15 min) near the shores between 10 and 50 cm depth. The sampling was done manually with a sieve between 10:00 AM and 11:00 AM, always by the same person. Data on temperature, oxygen saturation and pH were recorded in order to determine their influence on the fluctuations of density in each habitat. They were taken at the same time as the sample at 10:00 AM from the surface.

RESULTS

The growth parameters of all species are shown in Table 1. The growth curves are shown in Fig. 2. It can be observed that *Biomphalaria havanensis* and *B. helophila*, and *Pseudosuccinea columella* as well, grow more rapidly than *Planorbella duryi*. *Fossaria cubensis* had the slowest growth rate.

Data on temperature, oxygen saturation and pH of the ponds in which density studies were carried out can be seen in Fig. 3. The variation of densities are shown in Fig. 4. *Drepanotrema* spp. had the highest densities and bred during the whole period, as can be seen because of the high amount of newborn snails in each sample. Reproductive peaks of *Fossaria cubensis* and *Physella cubensis* in Mosquito Pond in February and March may have some influence in the diminution of densities of *Drepanotrema* spp.

DISCUSSION

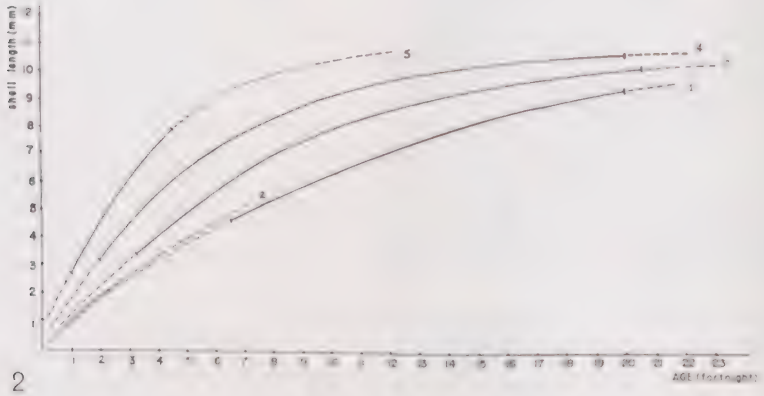
The growth parameters as well as the growth curves indicated that the two species of *Biomphalaria* grow more rapidly than *Planorbella duryi*. Former studies about drought resistance (Perera & Yong, 1983) showed that *Biomphalaria* spp. resist desiccation better than *P. duryi*; thus, its use as a competitor in temporary ponds may not be as successful as expected.

The variation of abiotic factors measured do not seem to have great influence in the density of the pulmonate snails. The changes in percentage of oxygen saturation are mainly due to the predominance of photosynthesis over respiration during sunny days, because of the dense vegetation of the ponds.

It is interesting to note the high density of *Biomphalaria helophila* found in Mosquito Pond after a long drought, most of which were newborn snails. Former studies showed that this species had the highest survival percentage among pulmonates after 18 months of diapause (Perera & Yong, 1983); and, as it can be seen, it is the best suited to repopulate this habitat after drought. This is evidence against the effectiveness of *Planorbella duryi* as a

TABLE 1. Values of the parameter k (characteristic growth constant) and L_{oo} (size of the animal for a zero growth rate) from von Bertalanffy's equation. Interval between two successive measures (Lt and Lt + 1) is a fortnight.

Species	Locality	K	L_{oo}	Validity
Planorbella duryi	Treasure Lake	0.116	11.16	3.5 -10.3
Biomphalaria havanensis	Camagüira	0.17	11.12	3.1 -10.3
Biomphalaria helophila	Camagüira	0.122	8.61	0.99- 2.11
Fossaria cubensis	Batabano	0.07	12.42	4.6 - 9.5
Pseudosuccinea columella	Batabano	0.27	12.29	2.7 - 8.4



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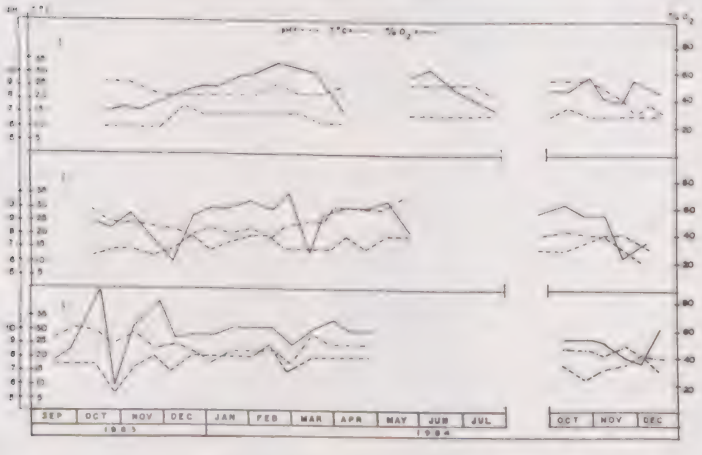

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FIG. 2. Growth curves calculated by the von Bertalanffy equation. 1 = *Fossaria cubensis*; 2 = *Biomphalaria helophila*; 3 = *Planorbella duryi*; 4 = *B. havanensis*; 5 = *Pseudosuccinea columella*. FIG. 3. Variation of abiotic factors in three ponds in which densities of pulmonates were studied. The measurements were made 10 cm from the water surface between 10:00 AM and 11:00 AM.

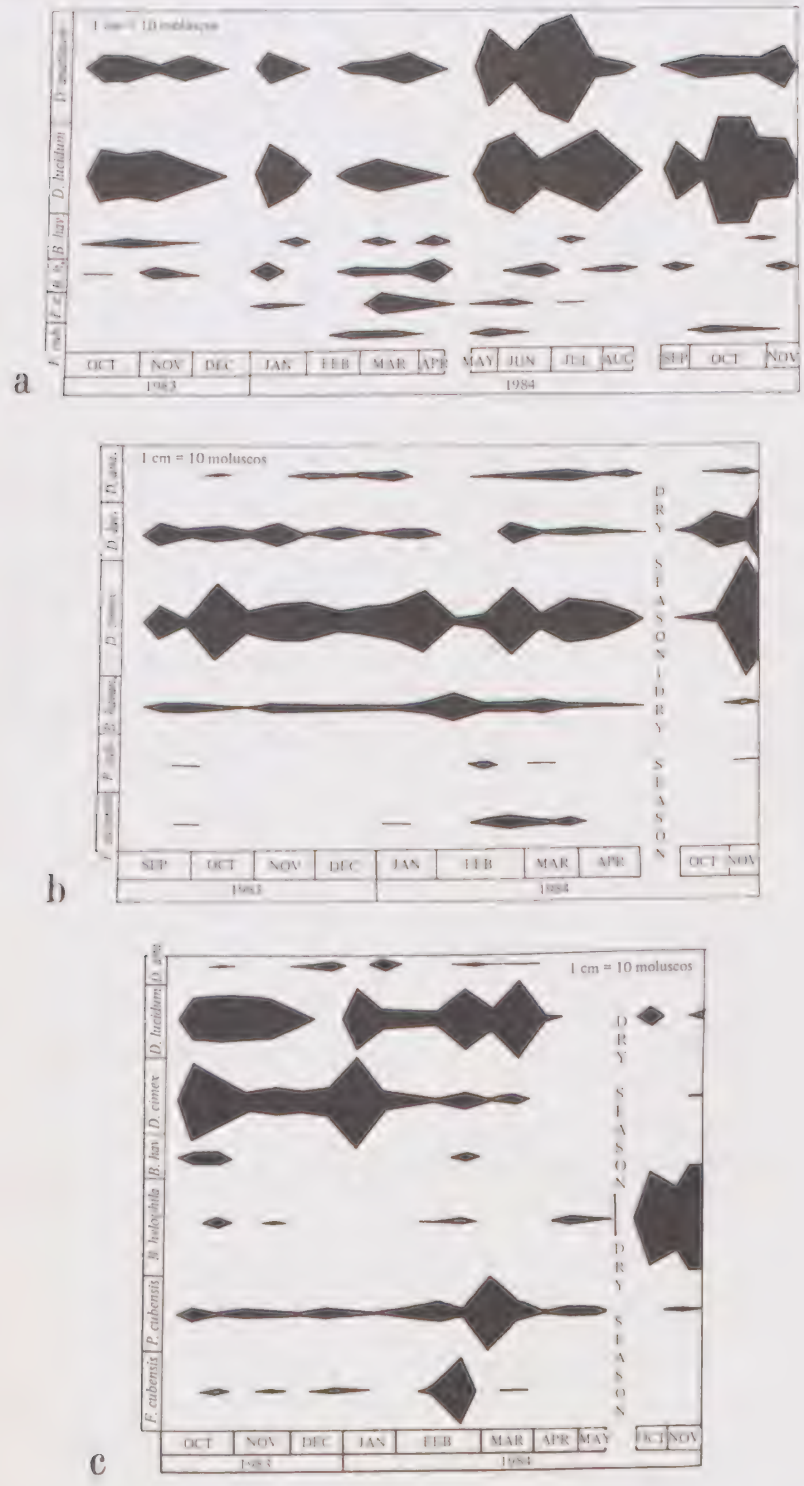

FIG. 4. Densities of pulmonates in **a**, Camaguira pond; **b**, Campo Florido; **c**, Mosquito Pond.

biological control agent in seasonal ponds.

In Camaguira and Campo Florido, on the other hand, *Drepanotrema* spp. were the snails that repopulated the ponds after the drought, maybe because in Camaguira the dry period was too short and in Campo Florido the soil retained some dampness due to the effect of *Typha dominguensis*.

ACKNOWLEDGEMENTS

We would like to thank Jean-Pierre Pointier for his valuable suggestions. This research was supported by the United Nations Development Programme/World Bank/World Health Organization Special Programme for Research and Training in Tropical Diseases.

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DESTRUCTION OF *INDOSUCCINEA SEMISERICA* (GASTROPODA: SUCCINEIDAE) EGGS BY THE BEETLE *CRYPTOBIUM FLUVIATILE*. – *Indosuccinea semiserica* (Gould) is a rare species with extremely localised distribution in lower West Bengal, India. The natural history of this hardwood tree-dwelling pulmonate snail is on record (Raut & Ghose, 1984). *Indosuccinea semiserica* lays gelatinous egg masses on the leaves of trees (*Citrus* sp.) during the monsoon season (July-September) in this part of West Bengal. The present note describes the destruction of eggs of this snail species by the beetle *Cryptobium fluviatile* Champ. Voucher specimens have been deposited in the National Collection of the Zoological Survey of India, Calcutta (Nos. M 22296/4 and 10130/H_4A, respectively, for *I. semiserica* and *C. fluviatile*).

Indosuccinea semiserica deposits 24-86 eggs in a brood. The eggs are round, transparent, gelatinous and, on the average, 1.8 mm in diameter. Due to their gelatinous nature, the eggs laid at a particular time adhere to each other in a single gelatinous mass.

Observations were made during July-September, 1983, at Budgebudge, 50 km south of Calcutta. During the day on 18 July, at the time of collection of newly hatched *Indosuccinea semiserica*, the author observed the beetle (*Cryptobium fluviatile*) feeding on the snail's eggs. A close inspection revealed the presence of a number of *C. fluviatile* insects on the branches and leaves of the same plant (*Citrus* sp.). Attention was given to the behaviour of a particular *C. fluviatile* moving on a leaf bearing the egg mass of *I. semiserica*. Within a few minutes, the insect succeeded in locating the egg mass. Initially, the insect moved over the egg mass touching the eggs with its mouth parts. This was followed with biting to cut open the egg membrane. The insect immediately started feeding on the egg mucus and made its way inside to reach the embryo, which was quickly consumed. The insect apparently had no interest in the rest of the egg mucus and moved away to attack another egg. The process was repeated and four to six embryos were eaten in a few minutes. In instances where the embryo was located close to the egg membrane, it was seized immediately after puncturing the membrane and the remaining mucus was untouched. This suggests that the beetle's preference was for the embryo and that the mucus was consumed only to reach the target. Further, the insect destroyed two to three more eggs in each attack by simply damaging the egg membrane, but did not feed upon the eggs. Owing to this method of attack, a single *C. fluviatile* destroyed as many as six to nine eggs of *I. semiserica* in one occasion.

Ocypus olens, a Staphilinidae beetle, has been identified as an effective predator on *Helix aspersa* Müller in California and is recommended for biological control of this citrus pest (Orth et al., 1975; Fisher et al., 1976). From the present study, it is suggested that *Cryptobium fluviatile* plays a role in regulating *Indosuccinea semiserica* populations.

Acknowledgements. The author is grateful to Prof. K.C. Ghose, Department of Zoology, Calcutta University, for kindly reviewing the manuscript.

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DISEASE IN THE PESTIFEROUS SLUG *LAEVICAULIS ALTE* (GASTROPODA: VERONICELLIDAE). – The slug *Laevicaulis alte* (Férussac) is very common in the gardens and vegetable fields of India and has proved to be a serious agri-horticultural pest (Raut & Mandal, 1984). On 9 June 1985, while the authors were studying the ecology of these slugs at Deulti, Howrah, West Bengal, India, they observed leucodermic lesions in six individuals of different sizes. These slugs were collected and a careful examination revealed the leucodermic lesions to be equally common on the slugs' ventral surface (Fig. 1a,b). These specimens were released in a terrarium and maintained under simulated natural conditions for further observations. Within five days, the lesion had spread all over the body in most individuals. After two weeks, on 24 June, three slugs became inactive and stopped feeding for a period of three days and died. After that, the remaining three slugs died within a few days. Subsequent field observations during August-September of 1985 in the same locality revealed an increased number of individuals (at least 45%) with a similar type of lesion. In each visit, 26-76 dead slugs with severe leucodermic lesions were noted. Voucher specimens of the slugs have been deposited in the National Collection of the Zoological Survey of India, Calcutta (No. M 22294/4).

FIG. 1a. A slug with leucodermic lesions (the white areas) on its dorsal surface. FIG. 1b. Ventral views of a normal (A) and an affected (B) slug. Arrows point to lesions.

The symptoms of this disease resembled those described in the giant African snail pest *Achatina fulica* Bowdich by Zwaluwenburg (1955), Mead (1956, 1961, 1979), Srivastava (1966) and Raut & Ghose (1977) from different parts of the world. The slug-infested area at Deulti is also inhabited by *A. fulica*, but we failed to locate a single individual of *A. fulica* with leucodermic lesions during the study period. Since the symptoms are similar to those previously found in *A. fulica*, it is probable that the etiological agent is of the same kind or close to it. According to Dean et al. (1970), the bacterium *Aeromonas hydrophila* (=*A. liquifaciens*) is involved in the pathology of the disease syndrome in *A. fulica*. Isolation of the pathogen from *Laevicaulis alte* is in progress in collaboration with the microbiologists of Bose Institute, Calcutta. After the etiological agent has been discovered, it will be possible to throw some light on the mode of its transmission. Whatever the nature of the etiological agent, the disease appears to be very effective in reducing the *L. alte* population in Deulti. This type of disease is recorded for the first time in slugs.

Acknowledgements. The authors are thankful to the Indian Council of Agricultural Research, New Delhi, for financial assistance.

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PREY PREFERENCE AND CAPTURE BY *HEMIFUSUS TERNATANUS* (GASTROPODA: MELONGENIDAE). – Two species of Melongenidae, i.e., *Hemifusus tuba* (Gmelin) and *H. ternatanus* Swainson regularly are caught by Hong Kong fishermen trawling the northern continental shelf of the South China Sea and thus occur in local fish markets. The former is numerous, the latter more rarely encountered. Morton (1985) has demonstrated that *H. tuba* is a bivalve predator, preferring deep-burrowing species by dramatically everting the proboscis down the inhalant siphon of the prey. Other categories of bivalves are less preferred. Hamada (1974) and Ozawa (1981), respectively, report that juveniles of *H. ternatanus* feed on bivalves and on the trochid gastropod *Suchium* (= *Umbonium*) *moniliferum*. No information is available on adults, and this study investigates prey preference and the mechanism of prey capture in this species.

Prey preferences. Two large *Hemifusus ternatanus* (shell lengths of 24 and 33 cm) were kept with a sequence of potential prey items over a period of six months in the marine aquarium of the University of Hong Kong. Initially, *H. ternatanus* was presented with carrion of various origins: bivalves, gastropods, shrimps, crabs, echinoids and fish. None was consumed. Subsequently, *H. ternatanus* was given living specimens of polychaetes (*Ceratonereis*), echiuroids (*Ochetostoma*), sipunculans (*Sipunculus*), asteroids (*Archaster; Asterias*), echinoids (*Anthocidaris; Temnopleurus*), holothurians (*Polycheira*: *Holothuria*), crabs (*Epixanthus; Gaetice*), shrimps (*Metapenaeus*), actinarians (*Haliplanella; Cavernularia*) and gastropods (*Babylonia; Chlorostoma; Chicoreus; Turbo; Lunella; Cypraea*). None was consumed. Eventually, *H. ternatanus* was offered a range of bivalve prey species; these are identified in Table 1. Four individuals of each species were offered, but ultimately very few were consumed. Attacked first were specimens of

TABLE 1. The prey preferences of two adult predators, *Hemifusus ternatanus*, offered a choice of four individuals each of a range of bivalves. After week 12 when feeding seemed to have ceased, four additional *Pinna pectinata* were offered to the predators. Other than *P. pectinata* and *Amusium pleuronectes*, the three groups of bivalves correspond to the Categories 1-3 of bivalves earlier established as a feeding sequence of preferred prey for *H. tuba* (Morton, 1985).

	TIME (weeks)												
	PREY ITEM	1	2	3	4	5	6	7	8	9	10	11	12	13
	Pinna pectinata	o	o	oo										
	Amusium pleuronectes													
	Hiatula diphos	o		o							o			
1	Sinonovacula constricta				o									
	Tapes philippinarum													
	Glauconome chinensis													
	Scapharca globosa													
	Scapharca cornea													
2	Anadara granosa													
	Barbatia virescens													
	Perna viridis													
	Gelonia erosa													
	Circe scripta													
	Cyclina sinensis													
3	Katalysia japonica													
	Gafrarium tumidum													
	Caecella chinensis													

Pinna pectinata (Pinnidae), followed by, but with more difficulty, *Hiatula diphos* (Tellinidae) and *Sinonovacula constricta* (Solenidae). The *Pinna* were consumed within three weeks, but the *Hiatula* and *Sinonovacula* were still not all consumed even after 12 weeks. No other bivalves were attacked, not even the large widely gaping arks (*Scapharca* and *Anadara*) normally eventually attacked by *H. tuba* (Morton, 1985). To determine whether or not the predators had ceased feeding because the offered prey was unacceptable, four more *P. pectinata* were offered them at week twelve. These were consumed within one week. It seems therefore that *H. ternatanus* prefers shallow buried, widely gaping bivalves, notably pinnids, but also will attack deeper burrowing species as a second choice. This is in direct contrast to *H. tuba*, which prefers the latter to the former (Morton, 1985; Table 1). Both are unable to attack the shelf scallop *Amusium pleuronectes*, presumably because of a well-developed flight response in this bivalve (Morton, 1980).

Both species also attack damaged bivalve prey.

The prey capture mechanism. Like *Hemifusus tuba*, *H. ternatanus* attacks its prey by stealth. When a specimen of *Pinna* is encountered it is delicately examined first with the siphon and eventually with the head and cephalic tentacles. With an intact *Pinna* (Fig. 1), the head eventually locates the posterior gape, at the siphons. The head is then thrust into the inhalant siphon and the proboscis, presumably, everted, as in *H. tuba*. Presumably, because *H. ternatanus* does not feed on widely gaping arks, this has not been seen.

FIG. 1. *Hemifusus ternatanus* feeding upon a specimen of *Pinna pectinata*.

Hemifusus ternatanus took, on average, some 10 hours to consume a *Pinna pectinata* 22 cm long. Usually, all tissues were eaten. On one occasion, a damaged fan shell was given to *H. ternatanus*. This too was eventually attacked but in a different manner from intact prey. The crack in the shell was located by means of the siphon (Fig. 2), presumably because the predator could detect blood escaping from the

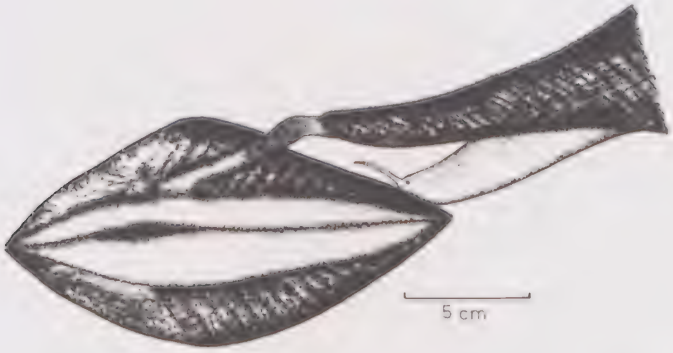

FIG. 2. *Hemifusus ternatanus* inspecting a damaged specimen of *Pinna pectinata*.

wound. Slowly and carefully the snail eventually inserted its siphon into the gap between the crack and proceeded to delicately probe for the strongest stimulus. Subsequently the siphon was removed and the bivalve grasped with the foot. The head then inspected the wound, cephalic tentacles delicately feeling every part of it. The head was then pressed into the crack and the proboscis everted (Fig. 3). Feeding commenced.

Discussion. The Melongenidae and related Buccinidae are often regarded as opportunistic scavengers (Dakin, 1912), though Nielsen (1975) reported that *Buccinum undatum* feeds principally upon bivalves. Taylor (1978) showed that polychaetes are important in the diet of *B. undatum*, though a wide range of prey items are consumed. Another buccinid, *Neptunea antiqua*, does, however, feed largely on bivalves (Taylor, 1978). In a Florida salt marsh, *Melongena corona* feeds on *Littorina irrorata* (Wilber & Herrnkind, 1984). The four western Atlantic melongenid whelks of the genus *Busycon* are principally bivalve

FIG. 3. *Hemifusus ternatanus* feeding upon a cracked specimen of *Pinna pectinata*.

predators (Colton, 1908; Carriker, 1951; Gunter & Menzel, 1957; Menzel & Nichy, 1958; Paine, 1963; Kent, 1983). Two major strategies are adopted. *Busycon spiratum* and *B. canaliculatum* largely feed on "active", gaping, bivalves (Magalhaes, 1948; Paine, 1962; Kent, 1983) by wedging the lip of their shell between the valves of the prey to prevent closing and to hold them sufficiently apart that the proboscis may be inserted. Conversely, *Busycon contrarium* and *B. carica* (as well as the fasciolariids *Fasciolaria hunteria* and *F. tulipa*) chip pieces from the valve margins of their preferred prey until a hole of sufficient size is made to insert the proboscis (Magalhaes, 1948; Carriker, 1951; Menzel & Nichy, 1951; Paine, 1962, 1963; Kent, 1983). Prey most frequently attacked in this way are completely closing, thick-shelled bivalves such as oysters and shallow-burrowing venerids and arks. Such prey items are defined as "passive" (Kent, 1983).

"Wedging" and "chipping" have never been observed in the South China Sea whelks; rather the prey is always approached with great care and deliberation. It is always grasped delicately by both species and the proboscis everted typically into the inhalant siphon. In the case of *Hemifusus tuba* feeding on *Sinonovacula constricta*, the act of eversion causes the prey's shell valves to close forcefully, often breaking them, but this is not "chipping". Differences in prey preferences between the two melongeniids are apparent, however. For *H. tuba*, Morton (1985) showed that bivalve prey fell into a number of categories according to morphology and life style. Most preferred prey (Category 1) were deep-burrowing, thin-shelled, posteriorly gaping solenids (e.g., *Sinonovacula*) and tellinids (e.g., *Hiatula*), with the proboscis being everted down the inhalant siphon. Such bivalves come under the definition of "active" (Kent, 1983). Preferred next (Category 2) were shallow-burrowing, thick-shelled species which, with no ventral mantle fusions, typically are widely gaping (e.g., *Scapharca, Anadara, Barbatia*). A third category of bivalves, shallow burrowing, thick shelled, but with extensive mantle fusions, rarely were successfully attacked (e.g., *Geloina, Circe, Gafrarium*). Any damaged bivalves (Category 4) were attacked opportunistically. *Hemifusus ternatanus*, however, prefers pinnids, i.e., "passive" prey which is surface dwelling, endobyssate and with an extensive posterior gape. Strangely, such pinnids would be categorised with shallow-burrowing arks attacked by *H. tuba* as a second choice, but on which *H. ternatanus* appears incapable of feeding. Adult *H. ternatanus* apparently have a more specialized diet than *H. tuba* and which importantly includes pinnids. Wang (1964) has shown that nine species of Pinnidae occur on the Chinese continental shelf, all extending from the lower intertidal to depths > 100 m. Both whelks are, however, opportunistic in that they will feed on damaged bivalves they encounter. Detection is by means of the siphon, which is sensitive both to blood in the water and to the streams of water posteriorly entering and leaving the mantle cavity of the prey. Further inspection of the prey is by the head and cephalic tentacles. Both species have much reduced eyes, and for both species the processes of prey detection, inspection and attack are coordinated by mechanical (and probably also chemical) stimuli. Preparations of the *H. ternatanus* radula establish that the structure of an isolated row of teeth is stenoglossate and comprises a tricuspid central tooth and lateral teeth with two strongly curved cusps. Differences in radula structure between *H. ternatanus* (Fig. 4A) and *H. tuba* (Fig. 4B) are that the central tooth has outwardly directed lateral cusps and the central cusp is unequally bifurcate terminally in the former but not the latter. The inner cusp of the lateral teeth is more delicate in *H. tuba*, being more blade-like in *H. ternatanus*.

FIG. 4. Camera lucida drawings of single rows of radula teeth of A, *Hemifusus ternatanus* and B, *H. tuba*.

A voucher specimen of *Hemifusus ternatanus* has been lodged in the collections of the British Museum (Natural History) (Reg. No. BM(NH)1985006).

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LABORATORY MAINTENANCE, NARCOTIZATION AND INDUCTION OF AESTIVATION OF APPLE SNAILS (MESOGASTROPODA: PILIDAE). – In a recent systematic and molecular genetic study of Thai apple snails, it was necessary to maintain large numbers of the snails in the laboratory for experimental purposes and for morphological studies. Because of the considerable numbers of specimens needed and the large size of these snails (the Pilidae are the largest of the freshwater snails, some species reaching a length of nearly 10 cm), aquarium space became critical, and narcotization methods used for smaller snails needed to be modified. Successful methods for dealing with these problems are described below.

The maintenance of *Pila* in the laboratory. *Pila* snails may need to be maintained in the laboratory for both short and long periods, depending on the purpose for which the snails are being kept. In my work, snails used in electrophoretic studies were needed for only short periods of time (1-2 months) before they were sacrificed. These snails were maintained in round aquaria 25 cm in diameter and 19 cm in height. The number of snails per aquarium did not exceed six if the snails were large (4-8 cm in width), and did not exceed 12 if the snails were small (2-4 cm in width).

Snails needed for longer periods were kept in very large aquaria (40 x 70 cm) in which there was a mud slope that provided an area for aestivating and resting. These aquaria could accommodate at least 15 large snails each.

The water used for maintaining the snails was tap water, which was left standing for at least 3 days in a large household cement tank. Water used for maintaining snails was taken only from the top and middle of the tank. The aquaria were not filled to the top, but enough space was left for snails to crawl above the water surface. The water in the larger tanks did not cover all of the mud slope, because the aestivating snails needed the mud bank above the water line. The water in the aquarium needed to be clean because the snails were very sensitive to their own wastes. Dead snails were removed immediately. Dirty water was drained off and replaced with clean water. The snails had to be handled gently during the changing of the water; otherwise, they would die.

Lids of the aquaria were closed tightly to prevent the snails from crawling out. Sometimes a stone had to be placed on the lid, because otherwise large snails such as *Pila ampullacea* (Linnaeus) and *P. angelica* (Annandale) could move the lid off the container.

Light was provided by a 15-watt cool, white fluorescent tube, which illuminated the aquaria for 10 hrs each day. During night, the snails were kept in the dark. Light also was used to wake the snails from aestivation. The aestivating snails that were put into the water could be activated faster if they were exposed to light.

Aeration was provided by a line from an air compressor. If the water was not well aerated or if it was too dirty, the snails would climb up above the water surface, or they would close their apertures tightly with their opercula.

Temperature in the aquarium room was maintained during 10 hrs of the day at 24-27°C by an air conditioner. In the evening and at night, when the outside air was cooler, the air conditioner was turned off, and the windows of the room were opened so that natural air could circulate through the room.

Food for the snails was of three kinds: commercial fishfood flakes, fresh lettuce and diatoms. The fishfood flakes were bought from a pet store or market, and a small amount of the flakes was supplied to the snails three times each week. This food contained mostly protein, lipid and fiber.

A small piece of fresh lettuce was supplied at the same time as the fishfood flakes. Due to the large size of the snails, they needed a relatively large amount of food to support their activities. The lettuce could supply the snails with enough carbohydrate and fiber without fouling the water. Two or 3 ml of diatoms (*Navicula* spp.) from a laboratory culture were placed in each aquarium once a week. The diatom cultures were supplied by the Southeast Asian Center for Applied Malacology and Entomology. The diatoms provided valuable nutrients, which might not occur in the fishfood flakes and lettuce, and which might be needed for snail growth.

Narcotization and preservation of *Pila* snails. In the laboratory, some of the snails were preserved to be used for anatomical studies. However, anatomical studies on preserved snails were augmented by observations on living snails (where colors of the organs were fresh and bright). Prior to manipulation, both fresh and aestivating snails had to be relaxed and narcotized to extend their head-foot region. The internal organs of the snails then could be uncoiled and prepared for dissection.

For narcotization, menthol alone could not sufficiently relax the snails; the snails would withdraw their head-foot region into the shell when being manipulated. Another chemical, sodium pentabarbitone (Nembutal), also was applied to the snails; it was more effective than menthol. But, as mentioned by Mutani (1982), many aquatic snails are sensitive to handling when using only Nembutal alone. Mutani used a combination of Nembutal and MS222, but for narcotizing *Pila* snails I used Nembutal combined with menthol, because this combination was more economical. I observed that there was some variation in the snails' sensitivity to the chemicals, depending on their behavior and geographic origin.

The snails to be narcotized were placed in a square plastic container (25 W x 45 L x 10 T cm). Ten large snails (*Pila ampullacea, P. angelica, P. pesmei* (Morelet) or *P. polita* (Deshayes)) or 20 small snails (*P. gracilis* (Lea) or *P. pesmei*) were kept in 4,500 ml of dechlorinated water for about 1-3 hrs. Handling the

snails made them close their opercula tightly. One hour normally was sufficient for newly collected snails to be active. But, aestivating snails needed about 3 hrs to wake up and move freely. A 60-watt light bulb exposing the water containing the snails would help them activate faster. The snails were arranged so that they would have enough room to move and then 12-15 small pieces of menthol flakes quietly were put on the water and a glass lid placed on the container, leaving a small space uncovered. The lid was necessary to keep the menthol vapors from dispersing. The small space between the lid and container was necessary, because if the menthol was too strong and there was no air circulation, the snails closed their opercula again. The snails were kept in the water with menthol for 1 hr before the addition of Nembutal. One ml of Nembutal was injected into the water every other hour. *Pila angelica* and *P. gracilis* needed 5 ml of Nembutal in 4,500 ml water, which made a 0.11% solution of Nembutal. Relaxation of the snails took about 24 hrs, after which time the snails were transferred to 5% formalin at 60°C. The snails were left in formalin for 2 hrs and then transferred to 70% ethyl alcohol.

Aestivating snails and snails from the central, north and northeast provinces of Thailand were able to withstand prolonged desiccation. To narcotize these snails, a higher concentration of Nembutal was needed and a longer time. *Pila ampullacea, P. pesmei* and *P. polita* needed 10 ml Nembutal in 4,500 ml water (0.22% Nembutal), and the relaxation time was 2 days. However, sometimes the snails were insensitive to the chemicals and needed 1 or 2 more ml of Nembutal in addition to the previous 10 ml Nembutal. The period of time would then be 50 hrs for narcotization.

Inducement of aestivation. During off seasons, *Pila* snails are difficult to find. For example, during the dry or winter season (November to February), it is hard to collect large numbers of *P. ampullacea*, so it is advantageous to get as many as possible when they are very common during the summer and rainy seasons. But, having large quantities of such big snails causes a problem regarding space; they need very large aquaria. To solve the problem of space, as well as maintenance labor, the snails were induced to aestivate in the aquarium room.

Thirty to 40 snails, depending on their sizes, were placed in a plastic basket (40 cm wide x 55 cm long) full of wet mud. Not all snails in a population could be induced to aestivate. Only snails which had previous experience of aestivating, as indicated by their having a white scar on their opercula, were used in this method. These snails were kept in pond water for a day, for they consumed much water. The snails, turned with their opercula upward, were pressed into the sticky mud until the opercula were at the same level as the mud, and a little mud was wiped on the opercula. The basket was then covered with a piece of thin cloth and secured with a string. This prevented the snails from crawling away. The baskets were labeled and placed on shelves exposed to a fluorescent lamp for 10 hrs a day. Mud gradually was drained of water and was dry within four weeks. The snails that did not aestivate would die and had to be removed. Dead snails had loose opercula which sank into the body whorl when pressed. When the opercula of live snails were pressed, the snails withdrew them more tightly into the aperture.

Acknowledgements. I wish to thank Drs. E.S. Upatham and J.B. Burch for facilities, and the World Health Organization and the Hinsdale Scholarship Fund, Museum of Zoology, The University of Michigan, for financial support.

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A COMMENSAL RELATIONSHIP BETWEEN *RYSSOTA* (PULMONATA, HELICARIONIDAE) AND A BEETLE IN THE PHILIPPINES. – During the collection of terrestrial mollusks near Caramoan Municipality, Camarines Sur Province, Luzon Island, Republic of the Philippines, in July 1981, an unusual commensal relationship between a land snail and a beetle was discovered.

Although not overly abundant, the large (ca. 10.0 cm greatest shell diameter, ca. 20.0 cm body length) helicarionid snail *Ryssota uranus angulata* (Möllendorff) (Fig. 1) is a remarkable member of the terrestrial mollusk assemblage. During daylight hours this species is most commonly found among leaf litter in large limestone solution pits. It becomes active shortly after nightfall, feeding on fallen, yellowing tree and shrub leaves. On virtually every *Ryssota* found, the small (ca. 5.0 mm) staphylinid beetle *Zyras sagax* (Cameron) (Fig. 2) was present.

FIG. 1. *Ryssota uranus angulata* (scale = 10 mm).

FIG. 2. *Zyras sagax* (scale = 1 mm).

In May 1983, my brothers, Garth and Troy, collected several specimens of *Ryssota otaheitana* subsp. on Mt. Isarog (1966 m), Camarines Sur Province, Luzon Island, at 1500 m. *Zyras sagax* was present on these snails also. These beetles were dark brown and apterous (wingless), while those collected near Caramoan (40 m elevation) were lighter in color and brachypterous (short-winged).

In the Caramoan area, *Zyras sagax* most commonly was observed crawling on the dorsal surface of the foot of active *Ryssota* at night. As the snails were collected and began retraction of the foot, the beetles immediately ran into the large mantle cavity opening. As many as seven beetles were seen on a single snail.

A very similar relationship exists in Paraguay and southern Brazil between *Megalobulimus oblongus* (Müller) (Megalobulimidae) and *Zonocopris bucki* Arrow (Scarabaeidae) (Stein, 1867; Martens, 1868; Arrow, 1932; Bequaert, 1935, 1948). Bequaert (1948) reported that the only information available on this relationship is that this beetle lives on the snail itself, feeding on the snail's mucus and is withdrawn under the mantle when the snail retracts. Robert W. Woodruff (pers. comm.) stated that *Z. bucki* probably does not feed on mucus, but utilizes the snail's feces for food and egg deposition.

Although time constraints did not allow study of the relationship between *Ryssota* and *Zyras sagax* in depth, several hypotheses can be entertained. *Zyras sagax* probably feeds on mucus produced by the snail. It is clear that the mantle cavity provides excellent protection from predation. It is possible that the beetles are utilizing the snail's feces in some manner, such as food or deposition and incubation of eggs. Long-term life history studies of both *Ryssota* and *Z. sagax* are needed to understand fully this relationship.

In addition to the beetles, several of the Mt. Isarog *Ryssota* were carrying a macrochelid mite (*Geholaspis* sp.). These mites were found in small clusters on the dorsal surface of the foot, and possibly were utilizing the snail as a means of transportation, not as a food source (Harold A. Denmark, pers. comm). The mites were not found on any *Ryssota* collected in the Caramoan area.

Voucher specimens of *Ryssota* are housed in the Florida State Museum. Specimens of *Zyras sagax* were deposited in the Florida State Collections of Arthropods (FSCA) and the British Museum (BM 1985-351).

Acknowledgements. I wish to thank the U.S. Fish and Wildlife Service and the New York Zoological Society for herpetological grants (to Walter Auffenberg) that allowed me the opportunity to collect terrestrial mollusks in the Caramoan area. The Philippine Parks and Wildlife Office was very helpful in issuing collecting permits. Robert E. Woodruff and Harold A. Denmark of the Florida Division of Plant Industries, Gainesville, provided identifications and insight in their respective fields. G.W. Krantz, Department of Entomology, Oregon State College, Corvallis, provided the generic determination of the mite. The time-consuming identification of *Zyras sagax* performed by Howard Frank, Florida Division of Plant Industries, Vero Beach (presently of Gainesville), is greatly appreciated. Special thanks go to my father, Walter Auffenberg, for bringing this relationship to my attention and for his continual support, and to my brothers, Garth and Troy, for their enthusiastic fieldwork.

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THE REDISCOVERY OF *POMATIOPSIS LAPIDARIA* IN NEW ENGLAND. – The range of the mesogastropod snail *Pomatiopsis lapidaria* (Say) (Pomatiopsidae) in northeastern North America has been reviewed by many authors. The more comprehensive treatments of the species (Abbott, 1948; Dundee, 1957) list eastern New York (Hudson River system) as the northeastern range limit along the Atlantic coastal plain. This view is shared in both regional (Baker, 1928; Harman & Berg, 1971) and general (Burch, 1982) studies on North American snail distribution. Despite these accounts, there is an historical record for *P. lapidaria* in Connecticut (New England) by Linsley (1845), who gave the locality as only "Housatonic". Jacot (1923) attempted to find this species along the Housatonic River in Connecticut but was unsuccessful. Three small shells (ca. 3 mm in shell length) of what appear to be *P. lapidaria* were collected by H.W. Winkley prior to 1900 from Branford, Connecticut (Quinnipiac River drainage, New Haven County), which is just east of the Housatonic River Drainage. These specimens are presently in the Museum of Comparative Zoology, Harvard University (MCZ 34044). The identification of these specimens is based on characters of the shell and operculum only. Recently, Jokinen & Pondick (1981) and Jokinen (1983) listed *P. lapidaria* as a rare component of the snail fauna of the Housatonic River drainage of Connecticut, but reported no recent collections.

During June, 1985, a survey of mollusks of the upper Housatonic River drainage revealed a population of *Pomatiopsis lapidaria* in Schenob Brook, Sheffield, Berkshire County, Massachusetts. The population subsequently was sampled twice (15 July and 14 October, 1985) and specimens were retained for examination. Both dry shells and relaxed preserved specimens have been placed in the Invertebrate Division, Museum of Zoology, University of Massachusetts, Amherst (UMA MO-1562). Additional voucher specimens (dry shells) have been deposited in the Museum of Comparative Zoology, Harvard University (MCZ 296080).

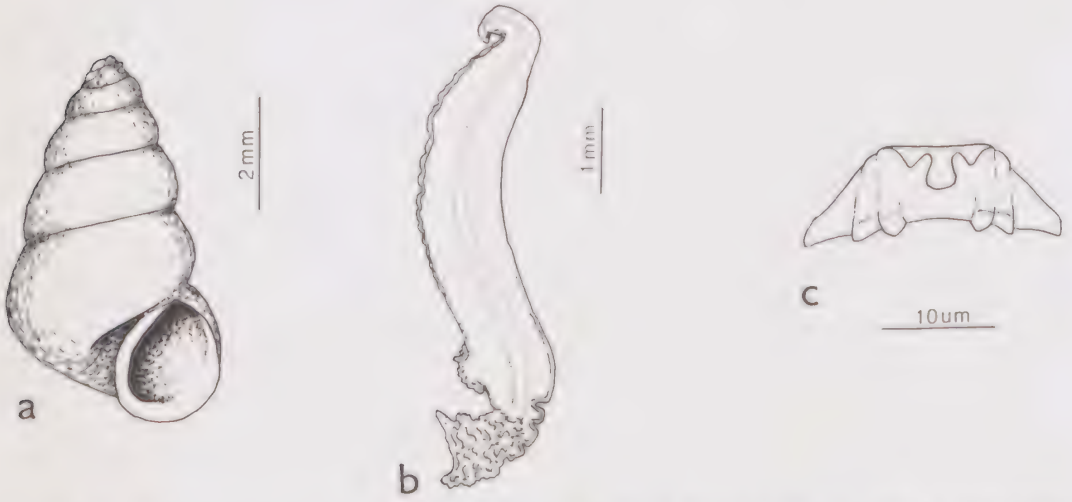

FIG. 1. *Pomatiopsis lapidaria* from Schenob Brook, Sheffield, Massachusetts. A, Shell; b, male verge; c, median tooth of the radula.

Identification of the specimens was determined by examination of the male verge, radula, and shell. All three collections were dominated by shells with shell lengths in excess of 4 mm. Among the three collections, the following maximum shell lengths (in millimeters) were recorded (three specimens per collection): 5 June – 6.5, 6.8, 7.1; 15 July – 6.3, 6.3, 6.7; 14 October – 6.1, 6.4, 6.9. These measurements compare well with Dundee's (1957) reported maximum shell lengths for Michigan specimens collected at similar dates. The latter two samples (July and October) contained several young of the year (<3 mm shell height). Dundee (1957) reported juveniles in Michigan populations during similar periods. Location of egg capsules was not attempted in this study. The sampled population was confined to low muddy banks with extensive growths of sensitive fern (*Onoclea sensibilis*). The only other living mollusk detected in the same habitat was the amphibious pelecypod *Pisidium casertanum* (Pisidiidae).

Acknowledgements. I thank Dr. Kenneth J. Boss for permitting access to malacological collections at the Museum of Zoology, Harvard University. I also thank Alan Richmond and Jenny Bush for their assistance in the field.

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A METHOD FOR RELAXATION OF INTERTIDAL MURICIDS. – During the recent dissection of many individuals of several species of intertidal prosobranchs, I found that none of the standard methods of relaxing these organisms and killing them in the relaxed state proved adequate. *Acanthina angelica* Oldroyd 1918 from the northern Gulf of California in particular proved difficult in this regard.

Finally, an attempt was made to duplicate the method of Carriker & Blake (1959), in which snails were immersed in 10 ppm of 1-napthyl N-methylcarbamate ("Sevin") in sea water. The sea water was put into an atmosphere of CO_2 evolved from dry ice. After 4 hrs, the snails were packed in dry ice for 24 hrs to insure their deaths in the relaxed state.

When this method was tried using *Acanthina angelica*, the snails began to retract slowly when they were removed from the Sevin, and more rapidly when placed on the dry ice, even when the relaxation period had been extended from 4 to 24 hrs. When the snails were removed from the dry ice packing after 24 hrs, they were found to be fully, or in a few cases almost fully, retracted.

The method that worked best for these snails was to put one to several snails in 30 ml of sea water. To this was added 0.1 g of technical grade Sevin crystals dissolved in 15 ml of acetone (Sevin does not dissolve well in water). The snails were kept in a dark, quiet place. Within 30 min, the snails began to relax. After 1 hr, 5 ml of 90% ethanol were added gradually without disturbing the water. Five ml of 90% ethanol were then added each half hour for the next 2½ hrs. After this, each snail was removed from the mixture and the shell was measured. After which, the shell was removed using a bench vise and forceps. Finally, each shell-less snail was placed in a separate container with 20 ml of sea water mixed with 10 ml of the Sevin/acetone solution, and the ethanol level was brought gradually to approximately 60% over a period of 4 hrs. At this point the snails ceased to respond, and they were fixed using either 70% ethanol or Bouin's fluid.

Another method that sometimes seemed to work even better was to tie the snails, apertures upward, by their shells to microscope slides using thread or rubber bands. This caused them to extend fully in an apparent attempt to right themselves, allowing them to be relaxed in a somewhat more extended state.

The slides with the snails tied to them were immersed for 1 hr in 30 ml of sea water to which had been added 0.1 g of Sevin dissolved in 15 ml of acetone. They were then moved to a fresh solution identical to the first, and the ethanol level gradually was brought to 60% over a period of 6 hrs. When this is done, the shell must be removed very soon after death and before fixing or the stomach, digestive gland and gonads begin to decompose. Another problem was that a certain percentage of snails is able to break loose from the slides, necessitating that they be retied to the slides and put back in the solution. Because of these problems, I recommend the second method only when the first does not provide sufficient extension.

Killing the animals with ethanol is necessary because the Sevin and acetone do not actually kill the animals. It seemed to me that Sevin, used in far lower concentration to kill insects, easily would kill gastropods. It further seemed that if this were not the case, the acetone would kill them or at least cause them to withdraw. For these reasons, I was skeptical when I read Carriker & Blake (1959), particularly when they suggested its use as an anesthetic for use on snails undergoing operations from which they subsequently would recover. I originally had hoped to use the Sevin/acetone solution for both relaxing and killing the snails, but found that *Acanthina angelica* gradually recovered after being immersed in the solution recommended in this paper for as long as two days and seemed to recover fully and move about normally in an aquarium. However, since these snails were killed and dissected 10 days after having been returned to the aquarium, I did not observe any long-term effects of Sevin/acetone treatment.

Carbamates, including Sevin, are reversible inhibitors of cholinesterase, which usually kill insects by inhibiting their respiration, and insects must ingest Sevin for it to be effective (George Ware, pers. com.). This suggests that Sevin might not be lethal to the animals in this study, because the Sevin/acetone solution suspended (rather than dissolved) in sea water may be taken up very slowly by the snails, as suggested by Dr. Ware (pers. com.). This may explain why the acetone has no apparent effect on these snails.

These two were the only methods I tried that were able to produce full relaxation in *Acanthina angelica* and in some cases caused the proboscis to evert. Unsuccessful attempts were made to kill *A. angelica* in an extended state using "Finquel" (Tricane Methanesulphonate), Epsom salts, menthol crystals, and novocaine.

Another method that has been used successfully for preparing muricids for dissection was to crack the shells using a vise without narcotizing them. Thereupon the columellar muscle was cut and the animal was fixed immediately (Shi-Kuei Wu, pers. com.).

The following prosobranchs have been killed in an expanded condition using one or the other of these techniques: *Acanthina lugubris* (Sowerby 1822), *Thais brevidentata* (Wood 1828), *Nucella emarginata* (Deshayes 1839) and *Cerithidea mazatlantica* Carpenter 1857. All of these species relaxed and died more quickly than *A. angelica*. They may, therefore, be left in each solution for a shorter period.

Acknowledgements. Rick Kretzinger, a Union Carbide Technical Representative, and Tom Merriam, a product specialist with Union Carbide in North Carolina, helped me to obtain technical grade Sevin.

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A CHAMBER FOR MONITORING GLOCHIDIAL INFECTIONS OF FISH HOSTS. – Determining the host-fish requirements of freshwater mussels (Bivalvia: Unionacea) is necessary to understand evolutionary patterns and processes within the group. The number of host-fish species (i.e., the degree of host specificity) coupled with the specific behavioral characteristics of the hosts during the glochidial release period (e.g., sedentary vs. vagile tendencies) can have a profound influence on freshwater mussel persistence and dispersal (Trdan & Hoeh, 1982). Variation in dispersal capability (and therefore in potential levels of gene flow) can help to explain interspecific variation in distributional patterns, levels of geographic differentiation, and colonization potential (Kat, 1984; Kat & Davis, 1984). In addition, the identification of fish hosts is essential to any conservation-oriented freshwater mussel management plan (e.g., Sylvester et al., 1984). Since hosts for only approximately 20% of the Nearctic species of Unionidae have been identified (Fuller, 1974; Stern & Felder, 1978), it is obvious that much work remains to be done in this particular area of freshwater mussel life history. To facilitate this end, the Glochidial Infection Monitoring Chamber (GIMC) described here is designed to increase the efficiency of data collection from potential fish hosts.

The two major components of the GIMC are a 4 liter Erlenmeyer flask (Corning 4980) in which a centered, 8.5 cm diameter hole was cut in the bottom, and a 50 mm filtering funnel (Corning 6140) with all but 2 cm of the stem cut off (Fig. 1). The funnel was fastened to the neck of the flask with General Electric Silicone II Seal. To complete the chamber, 8.0 cm and 10.0 cm diameter clear plastic discs were cut to serve as a cover. Both discs had a centered hole bored through them that would allow for insertion of a two-holed No. 1 rubber stopper. Two short pieces of glass tubing were inserted through the rubber stopper, one to act as a connector for an air stone and one to act as a vent. The smaller of the two discs was placed on the bottom to insure that the cover would not slide when placed over the hole in the flask. Finally, a small piece of rubber tubing with a pinchcock attached was placed over the funnel stem. For our particular application, a metal and wood rack was constructed to hold 46 chambers (Fig. 2).

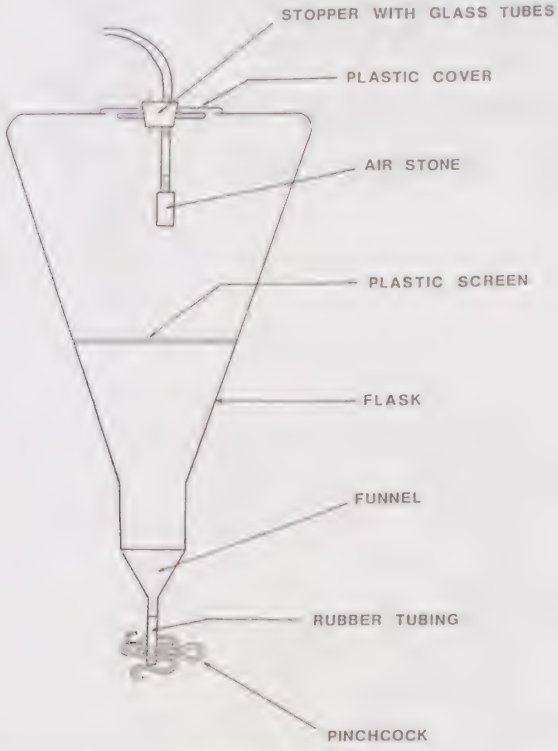

FIG. 1. A schematic illustration of the Glochidial Infection Monitoring Chamber (see text for details).

Naturally or laboratory-infected fish can be placed directly into the chamber. For certain fish (darters, for example) an optional semi-flexible, 12.5 cm diameter, plastic screen (7 mm grid) can be inserted into the chamber prior to the introduction of fish. This screen will prevent fish from getting trapped in the narrow end of the chamber while still allowing ample room for newly metamorphosed juvenile mussels, which are more dense than water, to fall to the bottom. Once fish have been placed in the chamber, sampling the bottom sediments for juveniles can be done on a regular basis. Routinely, about 20 ml of fluid is drawn off the bottom by release of the pinchcock. Samples can be checked immediately under a dissecting microscope or can be fixed in dilute formalin and investigated at another time. This procedure is much more efficient than siphoning bottom sediments (e.g., Zale & Neves, 1982) or decanting aquarium water into a large funnel (Trdan, 1976) as a means of detecting and concentrating juvenile mussels. This ease of sampling permits the precise determination of time courses for glochidial rejection and/or juvenile release from experimentally infected fish. Additionally, since a good estimate of initial glochidial infection intensity can be calculated with this apparatus (number of sloughed glochidia recovered + number of juveniles recovered), the

FIG. 2. Metal and wood rack holding 46 Glochidial Infection Monitoring Chambers. a, Front view; b, side view.

intrapopulational, interpopulational, and interspecific components of variation in host suitability (% of attached glochidia that complete metamorphosis; Kat, 1984) can be evaluated. This type of information is necessary to elucidate the ecological and evolutionary dynamics of the fish/glochidium association.

Acknowledgements. The construction of the above apparatus was made possible by a grant from the Living Resources Program and the Nongame Wildlife Program of the Michigan Department of Natural Resources. We also thank P.J. Moehs for assistance in the construction of the infection chambers, S.E. Cordoba for Fig. 1, and J.B. Burch for review of the manuscript.

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Malacological Review, 1986, 19: 121-122

OBITUARY
JOSEPH P. E. MORRISON
December 19, 1906 - December 2, 1983

On December 2, 1983, Joseph P. E. Morrison, one of this country's leading authorities on land and freshwater mollusks, died in Key West, Florida. He was well known to both professional malacologists and amateur collectors in the United States as a knowledgeable authority and a skilled and indefatigable field collector. Joe was a familiar and welcome figure at the annual meetings of the American Malacological Union, occasions to which he looked forward with keen anticipation.

Joe was born in South Bend, Indiana, on December 17, 1906, the son of Robert Ray and Lillian Byers Eldred, missionaries in the Christian Church (Disciples of Christ). When Joe was five years old, his father died in what was then the Belgian Congo (his mother had died in the previous year), and Joe and his two older brothers were adopted by Dr. Hugh T. Morrison, a physician in Springfield, Illinois.

Here Joe grew up, and early in his youth showed an interest in natural history. One day the family was walking in Springfield and young Joe had run on ahead. The family found him sprawled on the sidewalk, trying to pry loose a small shell he had discovered in the cemented conglomerate of the walk. The family story is that this was the start of his interest in shells.

As a boy, he explored the Sangamon River valley, its river and adjacent streams and woods, observing, learning and collecting. In the living room of Logan Place, the commodious Morrison home in Springfield, each boy had a corner where he kept his special treasures and favorite objects. Joe's corner had shelves with shells, stuffed birds, and other objects of nature. He enrolled in a correspondence course of taxidermy and learned the art of skinning and preparing bird skins, a skill that was to prove advantageous to him in later years.

He entered Transylvania College in Lexington, Kentucky, in 1922 at the age of 15 and, concealing his youthful age, played football there for two years. He stood 5 feet 10½ inches at that time and weighed about 185 pounds. Eager to obtain more advanced training in biology, he transferred to the University of Chicago in the fall of 1924. That fall he signed up for football to play under the great A. Alonzo Stagg, but, when Joe learned of the long and time-consuming practice hours demanded of players, he gave up football; he had come to the University to study, not to play football.

He graduated from the University of Chicago with a B.S. in 1926 and went on to get his M.A. and Ph.D. degrees at the University of Wisconsin. During this period he worked for two summers at the Illinois State Museum, and during his doctoral studies he spent his summers as zoologist on the Mt. Desert Island Biological Survey (1927, 1928) and as zoologist on the Wisconsin Natural History Survey (1929-1931). His dissertation was on the life history and biology of the freshwater snail *Acella haldemani* (Binney). While working towards his doctorate he was also graduate assistant and instructor at the University of Wisconsin.

After receiving his degree he held a position as Associate Professor in Biology at Crane Junior College, Chicago, for two years, from 1931 to 1933. When that institution had to close for lack of funds in

the depression years, most of its teachers were dispersed among the high schools of Chicago, Joe going to Kelley High School, where he taught for a year.

He married Dorothy Louise Dunn on February 6, 1930, and when the Morrisons came to Washington they had two daughters, Mary Louise and Lillian Dunn. A third child, Michael Paul Eldred was born in 1935 in Falls, Church, Virginia, where they lived until Joe's retirement.

In August of 1934, Joe joined the Divison of Mollusks, Smithsonian Institution, where he was to stay until his retirement in July 1975. As was the general custom in those days, he began as a Scientific Aide, spending much of his time performing the duties of preparator, cataloguer and technician.

Throughout his career at the Museum, Joe was interested in and studied numerous families of land, freshwater and brackish water snails. For many years he was especially attracted to those small land snails in the families Pupillidae, Zonitidae and Endodontidae, and he published several papers on them. He also published on the freshwater and brackish water families Hydrobiidae, Thiaridae, Ellobiidae, Siphonariidae and Unionidae. For his research on the Hydrobiidae, I remember he prepared an extensive file of 3 x 5 inch cards, each with a drawing Joe had made of the male intromittent organ of various species from his own dissections. He felt this to be an important diagnostic character for distinguishing genera in the Hydrobiidae, and he attempted to set up a classification based mainly on this character.

Joe was a devoted and skilled field collector, and in his earlier years, at least at the Smithsonian Institution, he spent many of his weekends and most of his vacations collecting, especially in the mid-Atlantic states, from New Jersey to the Carolinas and from the mountains to the sea. On all his travels to meetings of the American Malacological Union – and he attended all but seven meetings in the years from 1946 to his death – he always collected on his way to and from the meetings.

Joe was mechanically adept and skilled at fashioning his own tools and improving on his collecting and research tools. He built his own mechanical stage for his microscope and made his own fine forceps for handling delicate shells. He would proudly demonstrate the folding mussel bar for collecting freshwater mussels that he had designed. He was a collector of guns and a skilled gunsmith, experimenting with different loads of shotgun shells, testing them by means of the pattern made on paper targets. Joe Rosewater has told of many of these innovations (*Nautilus*, 1984, 98: 1-9). Some of Joe Morrison's older friends remember his rebuilt Ford car with the sloping hood; he called it an "Ord".

Nowhere, however, did Joe demonstrate his collecting enthusiasm, dedication and resourcefulness more than on his three trips to the central and south Pacific – to the atolls of Bikini in the Marshall Islands and to Raroia in French Polynesia. These trips, each lasting between one and four months, were carried out between 1946 and 1952. The mollusks that he brought back from these trips totaled about 12,300 lots and 220,000 specimens. This is a remarkable achievement when one considers that the total time spent on these expeditions came to about eight months, and that Joe collected not only mollusks, but other invertebrates, as well as lizards, birds and mammals, preparing the skins of the latter two groups himself.

As a result of these field trips to the tropical Pacific, and in preparation for a report on the mollusks of Bikini, he devoted much time to studies on some of the families of the larger and common marine mollusks of the Indo-Pacific. Among the byproducts of these researches is an unpublished manuscript on the Cypraeidae of Bikini, and a file drawer filled with folders containing notes on the systematics, morphology, biology and taxonomy of species of every family found on Bikini. The report on the marine mollusks of Bikini was never completed, but the great amount of information contained in these folders has been a valuable reference source for researchers using the collection of the Smithsonian Institution.

Joe's last Smithsonian-sponsored expedition was in 1965 to the Caribbean island of Dominica, where he took part in a biological survey of the fauna. He spent two months there and returned with a large collection of several thousand specimens. In the winter of 1966, Joe spent two months in Mexico, an excursion that was to be his last field trip outside of the U.S.A.

After surgery in December 1973, Joe found that he was increasingly unable to work with his accustomed zeal, and in July 1975 he retired from the Museum.

With the passing of Joe Morrison, a wealth of knowledge about mollusks, especially non-marine gastropods and bivalves, was lost.

Joe's memory remains bright with all who knew him as a friend and associate.

HARALD A. REHDER

Malacological Review, 1986, 19: 123-124

OBITUARY
ZINAIDA ALEXEYEVNA FILATOVA
(1905-1984)

On 11 June 1984 at the age of 78, Dr. Z.A. Filatova, one of the leading Soviet marine biologists, suddenly passed away. Dr. Filatova was one of the oldest scientists at the Shirshov Institute of Oceanology of the USSR Academy of Sciences, where she worked for over 40 years. Jointly with Academician Lev Alexandrovich Zenkevich, Dr. Filatova investigated the fundamental problems of recent bio-oceanology, i.e., the quantitative development of life on the bottom of the world's oceans and the global biological structure of the oceans. After Academician L.A. Zenkevich died, she headed the Laboratory of Benthos at the Institute from 1970 to 1979.

Dr. Filatova was one of the most competent malacologists in the world. She contributed greatly to the study of phylogeny, ecology, zoogeography and evolution of the bivalve fauna, particularly of the oceanic floor at great depths and in oceanic trenches. She published 120 works. She carried out extensive studies on the benthic fauna of the Barents, Kara and Bering seas, and reported, as a co-author, on investigations into general problems of marine biology in the monographs "Pacific Ocean" and "Oceanology". Dr. Filatova took part in many voyages of research vessels (the "Perseus", "Vityaz", "Akademic Kurchatov", etc.) at all latitudes of the world's oceans, from the Arctic to the Antarctic regions. Some of the expeditions were headed by her.

Dr. Filatova was an ardent propagandist of science. She delivered many lectures and reports in the Soviet Union and abroad. She lectured on marine biology in Austria, and took part in international oceanological and zoological congresses, symposia, and conferences in Australia, U.K., U.S.A., Canada, Denmark, USSR, Norway, Bulgaria and France.

Dr. Filatova was well known to her colleagues abroad. She was in correspondence with scientists of Denmark, U.K. and U.S.A., and enjoyed great prestige as a malacologist and marine biologist. She was a talented and enthusiastic teacher. She lectured on hydrobiology at Tomsk University. She was a supervisor and consultant to students, undergraduate and graduate.

Dr. Filatova was also involved in public activities. She was a member of the Soviet Women's Committee, and a member of the board of the USSR-New Zealand Society. For several years she was the chairman of the Section of Productivity of Marine Communities of the USSR National Committee of the International Biological Program (IBP) and a member of the IBP Subcommittee of Productivity of Marine Communities. Also, she was on the editorial board of the international journal *Malacologia*. For her scientific and public activities, Dr. Filatova was several times awarded honors by the Presidium of the USSR Academy of Sciences and by the USSR government.

Dr. Filatova was an outstanding and charming person. She was active literally up to her last day. When leaving the laboratory for the last time in her life she was discussing projects of future books and expeditions with her colleagues. She had a good knowledge of literature and art, was keen on photography and

drawing. Her joking drawings of episodes from the lives of marine biologists are known to her many Russian and foreign colleagues. Her scientific works are illustrated by her excellent drawings.

Dr. Z.A. Filatova was a considerate mother, grandmother of twin granddaughters, and was very fond of her little great-grandson. She was hospitable, kind, and interested in the fates of her disciples. Interesting talks on very different subjects attracted to her many friends who will always keep affectionate memories of her.

O.A. SCARLATO

Malacological Review, 1986, 19: 125-126

OBITUARY
JOSEPH ROSEWATER
September 18, 1928 - March 22, 1985

With the death of Joe Rosewater on March 22, 1985, at the age of 56, malacologists lost one of their most eminent and respected colleagues. Gone in the prime of life, he has left us not only the legacy of his accomplishments and contributions to science, but also memories of an ever-helpful co-worker and warm friend.

During the first seventeen years of his life Joe lived in Queens, Long Island, New York, where his father, also Joseph Rosewater, was an accountant with the City of New York. Joe was actually born in Claremont, New Hampshire, where Joe's mother, Alice Tipping Rosewater, had gone to be with her parents at Joe's birth. Joe was an only child, and when Joe was eight his father died, leaving his mother, a trained nurse, to bring up Joe alone. Part of the summers were spent with his mother's family in Claremont, New Hampshire, and on the shore of nearby Lake Sunapee. The visits to Lake Sunapee remained with Joe as a happy memory.

In April 1946, his mother died and two months later Joe graduated from the John Adams High School in South Ozone Park, Long Island. Before her death Joe's mother had appointed her brother Charles as Joe's legal guardian. That summer, therefore, Joe moved to his uncle's home in Claremont.

In the fall, Joe entered the University of New Hampshire at Durham, where he majored in zoology. In his junior year, his zoology professors, Emery F. Swan and George M. Moore, suggested that he take up a project in mollusks and that started his scientific collecting.

After Joe's graduation in 1950, he tried to find a teaching position or one in a museum, but because of the draft notice that he expected to receive at any time he was unsuccessful. He worked, therefore, for his uncle in Claremont until he received his draft notice in February 1951.

In that same month he married Mary Carlson of Gilmanton, New Hampshire, whom he had met while both were freshmen at the University of New Hampshire. In May he was sent to Fort Meade, Maryland, for basic training, and then to Fort Sam Houston, Texas, for training as a medical technician in radiology. In March 1952 he was sent to Germany, where for a little over a year he served in the 97th General Hospital in Frankfurt-am-Main.

When he returned to this country in April 1953 and was demobilized, he went to work at the Sacred Heart Hospital in Manchester, New Hampshire, as an x-ray technician. In addition, he was an instructor in biology at Mount St. Mary's college in nearby Hooksett, now New Hampshire College.

After two years in these positions Joe resigned and enrolled for the summer of 1955 in the University of New Hampshire Summer School. In the fall he entered the graduate program of the University. In June 1956 he graduated with an M.S. degree, his dissertation being *An illustrated key to the marine shelled gastropods of New Hampshire and adjacent coasts.* This paper was never published.

In the fall of 1956 Joe and Mary Rosewater moved to Cambridge, Massachusetts, where Joe entered

the Graduate School of Harvard University. By this time the family had increased to four, Katherine Louise having been born in 1954 and Gail Ann in 1956. A son, Carl Joseph, was to join the family four years later. In Cambridge they lived in the Harvard Graduate Student Housing complex.

For a little over three years Joe was one of Bill Clench's students, enjoying the congenial camaraderie that always existed between Bill and his students. From Bill and Ruth Turner he received a thorough grounding in all phases of malacology and in the necessary curatorial techniques.

Joe came to the Smithsonian in the summer of 1957 to spend three months in the Division of Mollusks as a summer intern. Here he carried out studies in the family Pleuroceridae for his doctoral dissertation. In the summer of 1958 Bill Clench took Joe with him on a collecting trip for freshwater mollusks through Kentucky, Tennessee and Georgia. To be with Bill on an extended field trip was an incomparable and memorable experience, and I know that for Joe this first expedition was an unforgettable event.

As the time for the completion of his graduate studies approached, Bill Clench wrote to me regarding the possibility of Joe joining the staff of the Division of Mollusks at the Smithsonian Institution. For a number of years we had been seeking approval to add a curatorial assistant in the Division of Mollusks, and we had on file a job application form that Joe had filled out a year or so earlier.

At this time the National Museum of Natural History was the recipient of a grant from the Office of Naval Research and Atomic Energy Commission to work up the marine faunas of the central tropical Pacific, particularly those of the atolls of Bikini and Enewetak in the Marshall Islands. Under this grant we were able to hire a malacologist and offered the position to Joe. On January 1, 1960, he entered on this position and thus began Joe's 25 years of devoted service to the Smithsonian Institution.

As a student under Bill Clench, Joe had taken for his doctoral project the study of a species complex in the genus *Pleurocera*. However, his first love had been marine mollusks, as he told me in a letter replying to my offer of the position under the ONR-AEC grant, and at the Museum of Comparative Zoology in Cambridge one of his tasks had been to incorporate Tucker Abbott's Philippine marine shells into the collection. During the months that he was on the ONR-AEC grant, Joe identified hundreds of lots of Indo-Pacific mollusks, most of them collected by Joe Morrison and others in Micronesia during the war years. He also helped reorganize the collections of Indo-Pacific mollusks, adding hundreds of lots to the collection and bringing up to date the arrangement and classification of that collection.

In the fall of 1961, we were able to offer Joe the position of Associate Curator and on October 2 he joined the staff of the Division of Mollusks. Having recently completed a study of the West Atlantic species of the Pinnidae, he started work on a monograph of the Indo-Pacific Pinnidae which was published in 1961. He began working on the family Tridacnidae and on the Littorinidae of the Indo-Pacific, which were completed and published in 1965, 1970 and 1971, respectively. He continued his interest in these two families, and at the time of his death Joe was working on the Littorinidae of the Eastern Pacific. He also had an interest in certain bivalve groups, especially the Periplomatidae and certain Leptonacean genera, particularly those commensal with other marine invertebrates.

Joe's field experience was wide and varied. In early 1963 he spent three weeks at the Enewetak Marine Laboratory in the Marshall Islands, and later in that year he was on the *Te Vega* in the eastern Indian Ocean for three months. These and later trips to Western Australia, the Moluccas, Tunisia, Ascension Island and Panama have been enumerated elsewhere (*Nautilus*, 1986, 100: 9-13). His last trips away from the Museum were to the Harbor Branch Laboratory at Fort Pierce, Florida, where he was carrying on field studies on *Periploma* and the Littorinidae.

Joe was a member of the American Malacological Union and he was its president in 1969. Other national organizations in which Joe was active were the Society of Systematic Zoology and the Paleontological Research Institute. Locally he was a president of the Biological Society of Washington and the fifth president of the National Capital Shell Club.

In the Museum, he was on several important committees, ably representing the Department of Invertebrate Zoology and the Division of Mollusks.

Joe is survived by his wife Mary, his three children and one granddaughter, Megan.

Joe's name and reputation will remain high in the history of the National Museum's Division of Mollusks, and his geniality and open friendliness long will be remembered by his fellow associates.

HARALD A. REHDER

Malacological Review, 1986, 19: 127-128

Photograph by R. Robertson.

OBITUARY
SIR CHARLES MAURICE YONGE
9 December 1899-17 March 1986

Charles Maurice Yonge was born on 9 December 1899 in Wakefield, Yorkshire, and was educated at Silcoates School where his father was the Headmaster. From school he passed in 1917 into the Army. Following the Armistice, he went to Oxford University in 1919 to read History. During that summer he decided to change his career to one in Forestry and went to Edinburgh University. Here he came under the influence of the comparative anatomist A.J. Ashworth and, in his second year, a period at the Millport Marine Station converted him to marine biology. The following year on a Plymouth Easter Course, his teacher was J.H. Orton, whose approach to the study of filter-feeding mechanisms was to have a profound influence on the young student. After graduation he was awarded the Baxter Natural History Scholarship (1922-24) and subsequently a Carnegie Research Scholarship (1924-25). At Edinburgh, now a comparative physiologist, he published in 1923 his first research paper on the mechanism of feeding, digestion and assimilation in the bivalve *Mya*, followed a year later by a comparably important paper on the crustacean *Nephrops*. To put his life's work in perspective, his last paper on the Mesodesmatacea, published in 1985 with J.A. Allen, crowned 62 years of original research and publishing.

In 1925, Maurice joined the staff of The Marine Biological Association of the United Kingdom (The Plymouth Laboratory) and there consolidated his growing reputation as a physiologist with a series of papers on molluscan digestion. One of these, on the oyster, published in 1926 remains today a classic account of feeding and digestion. Finely illustrated, it previsaged a long and fruitful association with the oyster and ultimately all its bivalve relatives. At Plymouth, his colleagues included Marie Lebour, F.S. Russell and Daphne Atkins, who at that time was researching the structure and systematic significance of the bivalve ctenidium. Such punctilious work reinforced by equally meticulous studies being undertaken in the United States by G.A. Drew, J.L. Kellogg and T.C. Nelson on bivalve feeding and digestion must have been enormously stimulating to the young scientist and subsequently affected his life's work. During 1924 and 1926, he undertook research at Naples, Villefranche, Trondhjem and Kristineberg and made the first detailed study of septibranch bivalves, in which we see a flair for functional morphology that he was later to refine with such impact. Maurice remained at Plymouth for two years before being awarded a Balfour studentship at Cambridge University, which enabled him to organise the Great Barrier Reef Expedition of 1928-29. Not yet 30, shy and with a speech impediment, Maurice was nevertheless appointed leader of the expedition, which comprised a party of 12 (including such life-long friends and colleagues as F.S. Russell, T.A. and A. Stephenson, Sidnie Manton, A.P. Orr, Sheina Marshall and his wife Mattie) and had a budget of £8,580.5s. The expedition was the turning point in Maurice's life, for it introduced him to the tropics and the rest of the scientific world to coral reefs. Based in a small laboratory at Low Isles for 13 months, Maurice not only organised the expedition but also assumed responsibility for the editing of the important repository of information contained in the reports it produced. Notwithstanding such demands on his time, Maurice initiated pioneer research with A.G. Nicholls on the physiology of corals. His first encounter with coral reefs resulted in a book, *A year on the Great Barrier Reef* (Putnam, London and New York, 1930), established his international scientific reputation, but also gave him a love of travel that allowed him to delve widely into the marine faunas of many parts of the globe. In later years, Maurice was also to participate in two other ship-borne expeditions to the Western Pacific and Great Barrier Reef, *Te Vega* (1965) and *De Moor* (1967). He returned to the Reef in 1975 as a participant in a research workshop to celebrate the opening of the Australian Museum's Lizard Island Laboratory. He celebrated his 75th birthday there with a visit

to Yonge Reef, named in his honour by the Australian Government.

Upon his return to the United Kingdom in 1929, Maurice rejoined the Plymouth Laboratory as a physiologist, this time investigating the origin and nature of the crustacean integument and egg case, but also broadening his views on feeding and digestion in the Metazoa.

In 1933, he was appointed Professor of Zoology at Bristol University, a position he held until 1944, during which time he made research visits to the Dry Tortugas and Herdla in 1934 and 1936, respectively. During this period, his interests turned more towards bivalve functional morphology, with important papers being published on the Tridacnidae and their symbiotic zooxanthellae, on the evolution of the swimming habit in the Bivalvia and the first interpretation of the Protobranchia. He also continued work on corals, following his visit to the Tortugas.

Maurice moved to Glasgow University as Regius Professor of Zoology in 1944, where he remained until his retirement in 1970. The move to Glasgow was tragically marred by the death of his first wife, Mattie, who had been with him on the Barrier Reef as Medical Officer. He was now, at this crucial time in his life, faced with the prospect of bringing up two children on his own. It was during this period that his interests in molluscs found renewed stimulus, though his researches were becoming less concerned with physiology and more and more with the evolution of structure and the interpretation of function. Such studies, particularly on the Tellinacea, Etheriidae, Chamidae and Carditacea, reviewed important groups, but he also synthesised ideas on the mantle, the byssus as a paedamorphic structure and on the evolution of the monomyarian and heteromyarian conditions. He published papers on scaphopods, the Polyplacophora and sustained a long interest in the Gastropoda, particularly those filter- and mucous-feeding prosobranchs, leading him into more general considerations of pallial evolution. In 1947, he published a short paper with T.C. Nelson on the development and phylogeny of the bivalve ctenidium. His first visit to the U.S.A. was to Berkeley and Pacific Grove in 1949. He enjoyed the west coast so much that he returned to it in 1956, 1960, 1966, 1969 and 1975 and published a series of papers on west coast bivalves and "limpets". During this period he was able to visit Bermuda (1951), Jinja (1953), Friday Harbor (1959, 1969) and Singapore (1969). In 1963 he published an important review on coral reefs in the first volume of *Advances in marine biology* (Academic Press, London and New York), which with F.S. Russell (a colleague on the Great Barrier Reef Expedition), he co-edited until his death.

Maurice's work on the evolution of the Bivalvia was acknowledged by the Royal Society when he was elected a Fellow in 1946 and was awarded the Darwin Medal in 1968. He was first Vice-President, and then President, of the Royal Society of Edinburgh, and he was made a C.B.E. (Commander of the British Empire) in 1954. Between 1964 and 1975 he made numerous visits to Discovery Bay, Jamaica, and developed a strong bond of friendship with T.F. Goreau, and from this partnership stemmed a series of papers on the physiology of coral and tridacnid zooxanthellae and the coral-boring mytilid, *Fungiacava*. The accumulated skills and knowledge of his travels and researches provided him with a wealth of information to use in more popular writings in marine biology. His writings during this period included a wide array of articles, and books on *British marine life* (Collins, London, 1944), *The sea shore* (Collins, new naturalist series, vol. 12, London, 1949), *Collins guide to the sea shore* (Collins, London, 1958), written in collaboration with J.H. Barrett, and *Oysters* (Collins, new naturalist series, vol. 18, London, 1960). Such volumes are framed by his first book, *The seas* (Wayne, wayside and woodland series, London, 1928), with F.S. Russell, and his last, *Living marine molluscs* (Collins, London, 1976), with T.E. Thompson. He was also able to help Anne Stephenson complete the life's work (*Life between tidemarks on rocky shores* (W.H. Freeman and Co., San Francisco, 1972)) of her husband, T.A. Stephenson. In 1966 he was to co-edit with K.M. Wilbur the two volumes of *Physiology of Mollusca* (Academic Press, London, San Francisco, New York), a significant treatise that for the first time attempted to bring together the expertise of workers in many different fields of molluscan research.

While at Glasgow, he succeeded as Chairman of the Executive Committee of the Scottish Marine Biological Association and was responsible for the development of the marine station at Millport on the Isle of Cumbrae and the transfer later to Dunstaffnage, Oban. From 1949-1967 he served as President of The Scottish Marine Biological Association, and in recognition of his many services to marine biology he was honoured with a Knighthood in 1967. His services to The Marine Biological Association of the United Kingdom were also long, for he served as a Vice-President from 1961 until his death.

He resigned from the Chair of Zoology at the University of Glasgow in 1964, but remained as a Research Fellow until 1970, when he was appointed Honorary Research Fellow in the Zoology Department of the University of Edinburgh until 1983. His travels continued: Friday Harbour (1975), Pacific Grove (1975), Singapore (1977), AIMS, Queensland (1978) and Hong Kong (1973, 1978). His researches and writings also continued, with papers on the Saxicavacea, Pectinacea and Anomiacea leading him to investigate the significance of the ligament in the classification of the Bivalvia with a review of cemented bivalves and new insights into the mantle margin. He worked at the level of the superfamily and few malacologists, now and tomorrow, will be able to work on any one of these taxonomic groups without reference to him.

Maurice accumulated honours. He held honorary doctorates from the Universities of Bristol, Heriot Watt, Manchester and Edinburgh, the last awarded in 1983 when the Royal Society of Edinburgh was celebrating its bicentenary and the University its four-hundredth anniversary. He was a member of numerous scientific societies worldwide, including the California Academy of Sciences, and was a welcome visitor to the great array of marine laboratories which he, in many cases, helped found. By 1983, however, Maurice was very ill with Parkinsonism, an illness which progressively debilitated him physically but not intellectually. Right up to his death, he was writing to friends about his continuing ideas on molluscan evolution. During his last years, he was lovingly cared for by his second wife Phyllis and their son Christopher.

Maurice's life of travel, teaching and research made him not just a fount of knowledge and advice but gave him a breadth of understanding that also made him a fascinating teacher and a warm, sympathetic and witty companion. He will be remembered not just as one of the great marine biologists and malacologists of this century, but also as one of the kindest and truest of men, who readily gave of his knowledge, experience and friendship and who has left behind when he died peacefully on the 17th March 1986 many who consider it a privilege to have known and been befriended by him. Even at 86, death has taken him too quickly.

BRIAN MORTON

NEWS AND ANNOUNCEMENTS

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FIRST INTERNATIONAL CONGRESS ON MEDICAL AND APPLIED MALACOLOGY. – The First International Congress on Medical and Applied Malacology will be held on 2-6 June 1987 in Monterrey, Nuevo León, México. The purpose of the Congress is to bring together workers dealing with mollusks as mediators of parasitic diseases of man and domestic and other animals, venomous mollusks, mollusks as agricultural pests, etc. The subjects that will be dealt with by the Congress are medical, veterinary and agricultural malacology, and will include topics on biology (ecology, taxonomy, distribution, genetics, etc.) of mollusk hosts and pests, mollusk-parasite relationships, parasite faunas of mollusks, snail control, etc.

Those interested in attending the Congress should contact M. en C. Fernando Jiménez-Guzman, Laboratorio de Parasitología, Facultad de Ciencias Biológicas, UANL, A.P. 22, San Nicolas de los Garza, Nuevo León México C.P. 66450.

INTERNATIONAL SOCIETY FOR MEDICAL AND APPLIED MALACOLOGY. – Recognizing the need for a malacological organization devoted specifically to the concerns of applied malacology, i.e., to medical, veterinary and agricultural malacology, a group of medical, veterinary and general malacologists meeting at Los Tuxtlas, Veracruz, México, initiated such an organization, the International Society for Medical and Applied Malacology. This organization will focus its attention on mollusks as mediators of parasitic diseases of man and other animals, and as pests to agriculture, materials, etc.

Annual dues for membership in the Society are US$35.00, and should be sent to the International Society for Medical and Applied Malacology, P.O. Box 2715, Ann Arbor, Michigan 48106, U.S.A.

The new Society will publish its own scientific journal, the *Journal of Medical and Applied Malacology*, and a biannual newsletter. Members will receive the journal and the newsletter free of charge. Institutional subscription is US$50.00 per year.

The Society also will sponsor congresses on medical and applied malacology at periodic intervals. The first congress will be held 2-6 June 1987 in México. Those interested in attending this congress should write to M. en C. Fernando Jiménez-Guzman, Laboratorio de Parasitología, Facultad de Ciencias Biológicas, UANL, A.P. 22 San Nicolas de los Garza, Nuevo León, C.P. 66450, México.

UNITAS MALACOLOGICA. – *Unitas Malacologica* is an international organization of malacologists and malacological societies whose goal is to support malacological research throughout the world and to regularly organize international malacological Congresses. The originally European society, founded in 1962 in London, was changed into a more broadly international organization in 1977 and now has more than 200 members all over the world. Its legal domicile is Basle, Switzerland. The annual subscription is 20 Swiss francs. This membership fee includes the Proceedings of the Congresses, held every third year. The last Congress was held in Edinburgh, Scotland, in 1986. The next International Malacological Congress will be held in Tübingen, F.R. Germany, in 1989.

Questions and applications with respect to membership should be sent to the Secretary, Dr. Edmund Gittenberger, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

NINTH INTERNATIONAL MALACOLOGICAL CONGRESS, EDINBURGH, 31 AUGUST - 6 SEPTEMBER 1986. – The Ninth International Malacological Congress was held in Edinburgh in 1986, from 31 August to 6 September. The scientific programme largely consisted of eight special Symposia. The programme included a Colloquium for Curators and a session on the European Invertebrate Survey, as well as the General Assembly of *Unitas Malacologica*.

The Symposia were as follows: History of Malacology [held jointly with the Society for the History of Natural History in its jubilee year]; C.M. Yonge Commemorative: Bivalvia; Higher Classification and Phylogeny of the Prosobranchia; Applied Malacology; Cold-water Mollusca: Arctic, Antarctic and Deep-Sea; Introduced Species; Evolutionary Biology of Opisthobranchia; and Molluscs as Threatened Species: Their Exploitation and Conservation.

TENTH INTERNATIONAL MALACOLOGICAL CONGRESS. – The Tenth International Malacological Congress will be held from August 27 to September 2, 1989, in Tübingen, Southwest Germany. Papers dealing with any aspects of malacology are invited for oral or poster presentation. Malacologists wishing to attend should be prepared to submit provisional titles of papers, together with one or two sentences

exposing the questions dealt with therein (instead of an abstract, for which it would be too early), before September 30, 1988.

Address inquiries to the current president of *Unitas Malacologica*: Dr. Claus Meier-Brook, Tropenmedizinisches Institut der Universitat, Wilhelmstrasse 31, D-7400 Tübingen, Federal Republic of Germany.

AMERICAN MALACOLOGICAL UNION ANNUAL MEETING, 1986. – The 52nd annual meeting of the American Malacological Union was held in Monterey, California, U.S.A., from 1 July to 5 July 1986. Dr. James W. Nybakken was the presiding officer.

AMERICAN MALACOLOGICAL UNION MEETING, 1987. – The 53rd annual meeting of the American Malacological Union will be held in Key West, Florida, from July 19 to July 23, 1987. For further information, contact William G. Lyons, 4227 Porpoise Drive SE, St. Petersburg, Florida 33705, U.S.A.

THE INSTITUTE OF MALACOLOGY held its annual meeting on 2 July 1986 in Monterey, California, U.S.A. Members present were J.B. Burch, Melbourne R. Carriker, George M. Davis, James W. Nybakken and Clyde F. E. Roper.

THE 1987 ANNUAL MEETING OF THE INSTITUTE OF MALACOLOGY will be held in Key West, Florida, U.S.A., just prior to the annual meeting of the American Malacological Union. For further details, contact Dr. James W. Nybakken, Moss Landing Marine Laboratories, Box 223, Moss Landing, California 95039, U.S.A.

MEETING OF THE SOCIETY FOR EXPERIMENTAL AND DESCRIPTIVE MALACOLOGY. – The 1986 annual business meeting of the Society for Experimental and Descriptive Malacology was held on 26 January 1986 in Ann Arbor, Michigan, U.S.A. For further information, contact Dr. J.B. Burch, Secretary-Treasurer of the Society, P. O. Box 3037, Ann Arbor, Michigan 48106, U.S.A.

THE KOREAN JOURNAL OF MALACOLOGY. – The Malacological Society of Korea has distributed Vol. 1, No. 1 of its new journal, *The Korean Journal of Malacology*. The first number contains 76 pages, plus six introductory pages, and includes five research articles, a review, the programs and abstracts of the first two meetings of the Society (held in 1984 and 1985) and announcements. One paper (Pyung-Rim Chung: "Malacological studies on *Parafossarulus manchouricus* (Gastropoda: Prosobranchia) in Korea") is in English. Unfortunately, all other articles are in Korean. However, the research and review articles have English language abstracts. For further information, contact the Secretary-General of the Malacological Society of Korea, Dr. Pyung-Rim Chung, c/o Department of Parasitology, College of Medicine, Yonsei University, CPO Box 8044, Seoul, Korea.

MALACOLOGY DATA NET. – This is a new serial publication which requests that authors submit manuscripts as "camera-ready copy", and to provide US$10.00 per page "page charges", if possible. Subscription price is US$14.50 per year in North America and US$18.00 per year outside North America. Inquiries should be directed to the Editor, Arthur H. Clarke, Ecosearch, Inc., 325 E. Bayview, Portland, Texas 78374, U.S.A.

COURSE IN NATURAL HISTORY OF INVERTEBRATES. – A field-oriented course in "Natural History of Invertebrates" will be taught by J.B. Burch at The University of Michigan Biological Station on Douglas Lake, Michigan, during the summer (late June to mid August) 1987. A prominent section of the course will deal with non-marine mollusks. For further information, write to Director, University of Michigan Biological Station, The University of Michigan, Ann Arbor, Michigan 48109, U.S.A.

HELDIA – MÜNCHNER MALAKOLOGISCHE MITTEILUNGEN. – A new malacological journal, *Heldia*, has been announced by the Münchner Malakologische Mitteilungen. The first issue will include the following articles: Hans D. Boeters, "Unbekannte westeuropäische Prosobranchia, 6"; Hans D. Boeters, "Zur Identität des *Bythiospeum*-Typus (Prosobranchia, Hydrobiidae)"; Hans D. Boeters, "Zur Identität des *Hydrobia*-Typus (Prosobranchia, Hydrobiidae)"; Gerhard Falkner, "*Stagnicola palustris* (O. F. Müller) vom Originalfundort"; Christa Frank, "Ein weiterer Nachweis von *Vaginulus (Sarasinula) plebeius* Fischer 1868 vom südamerikanischen Kontinent (Gastropoda, Veronicellidae)"; Dieter Müller & Gerhard Falkner, "*Potamopyrgus jenkinsi* (E. A. Smith) in Bayern"; Hartmut Nordsieck, "Eine neue *Triptychia*-Art aus dem bayerischen Oligozän (Gastropoda, Triptychiidae)"; Peter L. Reischütz, "Beiträge zur Molluskenfauna Niederösterreichs, VI"; Anton Stummer, "Eine neue Unterart der Höhlenschnecke *Zospeum alpestre* (Freyer) aus der Kupitzklamm bei Eisenkappel, Kärnten"; Jürgen Werner, "Pathologische Veränderungen bei *Helix pomatia* L. (Pulmonata, Helicidae)"; Kurze Mitteilungen.

For further information, write to Redaktion *Heldia*, Margrit Falkner, Raiffeinsenstrasse 5, D-8059 Wörth-Hörlkofen, F. R. Germany.

ARGONAUTA – JOURNAL OF MALACOLOGY. – A new publication has recently appeared entitled "*Argonauta*", with the subtitle "Journal of Malacology"; published by the Associazione Malacologica Internazionale, Via Case Basse, 171, 00126 Acilia (Roma), Italy. Subscription price per annum is US$16.00. The first issue (year 1, no. 1, Maggio 1985), containing 28 pages, contains three bilingual articles (in Italian and English), all illustrated in color: Raimondo Villa, "La famiglia Conidae nel Mar Mediterraneo"; Roberto Ubaldi, "Contributo alla conoscenza del genere *Nacella* Schumacher, 1817 nelle regioni Antartiche e sub-Antartiche"; Luciano Barbeini, "La famiglia Capulidae Fleming, 1822 nel Mediterraneo". Also included are some advertizements.

The second issue (year 1, no. 2-3, Settembre 1985) contains four articles: Roberto Ubaldi, "Il genere *Nacella* Schumacher, 1817" [continued]; Luciano Barberini, "La famiglia Bursidae Thiele, 1925 nel Mar Mediterraneo"; Salvatore Minghetti, "La famiglia Volutidae nel Mar Mediterraneo"; Roberto Ubaldi, "Famiglia Strombidae: Il sottogenere *Tricornis* Jousseaume, 1886. *Strombus oldi* Emerson, 1965, 42".

This publication appears to be directed mainly to shell collectors.

STUDENT FELLOWSHIPS IN THE SMITHSONIAN INSTITUTION. – The Division of Mollusks, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, announces the availability of two fellowships to be awarded to graduate students of systematic malacology: the Rosewater Fellow Award (up to $500) and the Smithsonian-COA Fellow Award (up to $1000). These awards are to help support students for short-term research visits to the collections and libraries of the Division of Mollusks, National Museum of Natural History, and are to be used for systematic studies of Mollusca. Funds can help cover travel, subsistence, and research costs [xerox, postage, etc.]. Interested students should submit a one-page proposal, a budget with indication of matching funding if available, and a supporting letter from their faculty advisors. Deadline for applications is March 1, 1987. Awards will be announced on April 1, 1987. Direct inquiries to Division of Mollusks, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

NEW MOLLUSK CURATOR AT THE UNIVERSITY OF MICHIGAN.–Dr. Douglas J. Eernisse has joined Dr. J.B. Burch as the second Curator in the Museum of Zoology's Mollusk Division. Dr. Eernisse also has an appointment as Assistant Professor in the Department of Biology at The University of Michigan. Before coming to The University of Michigan, Dr. Eernisse received his Ph.D. degree from the University of California at Santa Cruz, and completed a postdoctoral appointment at the Friday Harbor Laboratories, University of Washington.

SEND YOUR MANUSCRIPTS TO *MALACOLOGICAL REVIEW* ON DISKS.–Effective immediately, prospective authors submitting manuscripts to *Malacological Review* are encouraged to submit a disk version of manuscripts in addition to the normal paper copies. This will speed processing and reduce production costs. Disks can be either Macintosh or MS-DOS compatible and preferably in MacWrite, Microsoft Word or Wordstar formats, or saved from your word processor as a text (ASCII) file.

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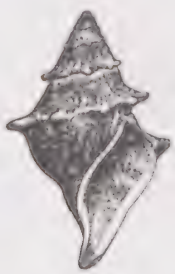

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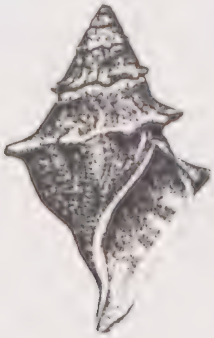

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der Senckenbergischen Naturforschenden Gesellschaft
Organ der Deutschen Malakozoologischen Gesellschaft

Begründet von Prof. Dr. W. Kobelt
Weitergeführt von Dr. W. Wenz, Dr. F. Haas und Dr. A. Zilch
Herausgegeben von Dr. R. Janssen

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der Senckenbergischen Naturforschenden Gesellschaft
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Begründet von Prof. Dr. W. KOBELT
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Frankfurt am Main 1986

ISSN 0003-9284

Basteria

ISSN 0005-6219

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Redactie-adres: Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Postbus 9517, 2300 RA Leiden.
De redactie wordt bijgestaan door een redactieraad van prominente malacologen.

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ISSN 0005 6219

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DE NEDERLANDSE MALACOLOGISCHE VERENIGING

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SPEDIZIONE IN ABBONAMENTO POSTALE - GRUPPO IV/70

Grafiche ATA - Paderno Dugnano
Finito di stampare nel Marzo 1985

Bollettino Malacologico

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Direttore Responsabile: Fernando Ghisotti

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Direttore Responsabile: Fernando Ghisotti

AUTORIZZAZIONE TRIBUNALE DI MILANO N. 479 DEL 15 OTTOBRE 1983
SPEDIZIONE IN ABBONAMENTO POSTALE - GRUPPO IV/70

Società Italiana di Malacologia
Viale Gadio, 2 - 20121 Milano (MI)

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COMUNICACIONES
DE LA
Sociedad Malacológica
DEL
Uruguay

MONTEVIDEO URUGUAY

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Published by Angus Graham Associates, 70-78 Queen's Road, Reading, Berks.

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Published by Angus Graham Associates, 70-78 Queen's Road, Reading, Berks.

Printed in England by L&D Printing Services, London Road, Sunningdale, Berkshire

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Published by Angus Graham Associates, 70-78 Queen's Road, Reading, Berks.

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NUMBER 3

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Philadelphia, Pa. 19103, U.S.A.

Published by

AMERICAN MALACOLOGISTS, INC.
P.O. Box 2255
Melbourne, Florida 32902-2255
U.S.A.

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ISSN 0028-1344

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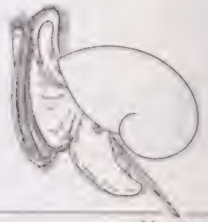

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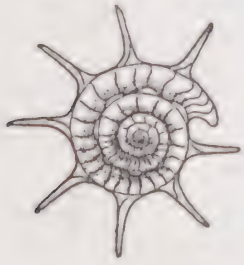
日本貝類学会

Published by
THE MALACOLOGICAL SOCIETY OF JAPAN

昭和61年7月 July 1986



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VOLUMES, ISSUES AND PUBLICATION DATES OF *MALACOLOGICAL REVIEW*. – *Malacological Review* was first published in one number for the year 1968. This single issue (187 pages) constituted Volume 1. For each of the years from 1969 to 1974 (Vols. 2, 3, 4, 5, 6 and 7), two semiannual numbers were published, each two issues for a calendar year constituting a volume. Beginning with Vol. 4 (1971), each of the two annual issues were formally designated as a "number", the first issue of each volume being "Vol. _, No. 1" and the second issue "Vol. _, No. 2". Beginning with Vol. 8 (1975), both issues for each calendar year were combined and designated as "Vol. _, No. 1-2". Each volume normally consists of about 220 pages.

Publication dates of past issues are as follows: Vol. 1, 7 June 1969; Vol. 2 [No. 1], pages 1-102, 10 June 1969; Vol. 2 [No. 2], pages 103-214, 8 May 1970; Vol. 3 [No. 1], pages 1-102, 28 May 1970; Vol. 3 [No. 2], pages 103-192, 13 March 1971; Vol. 4, No. 1, 27 July 1971; Vol. 4, No. 2, 10 February 1972; Vol. 5, No. 1, 31 July 1972; Vol. 5, No. 2, 12 January 1973; Vol. 6, No. 1, 12 April 1973; Suppl. 1, 25 October 1973; Vol. 6, No. 2, 29 January 1974; Vol. 7, No. 1, 3 July 1974; Vol. 7, No. 2, 30 September 1974; Vol. 8, No. 1-2, 15 May 1975; Vol. 9, No. 1-2, 26 March 1976; Vol. 10, No. 1-2, 3 March 1978; Vol. 11, No. 1-2, 20 July 1978; Vol. 12, No. 1-2, 21 December 1979; Suppl. 2, 31 October 1980; Vol. 13, No. 1-2, 30 April 1981; Vol. 14, No. 1-2, 22 July 1981; Vol. 15, No. 1-2, 4 May 1982; Suppl. 3, 15 July 1982; Vol. 16, No. 1-2, 1 February 1983; Vol. 17, No. 1-2, 11 April 1984; Vol. 18, No. 1-2, 20 December 1985.

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ERRATA, Vol. 18:

p. 61, second text paragraph, "Character 16" chould read "Character 15."
p. 70, third paragraph, "Consquently" should read "Consequently."
p. 124, last line, "RUTH J. TURNER" should read "RUTH D. TURNER."

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